Investigations into the functioning of phytoplankton, zooplankton, kelp and benthic communities at the Prince Edward Islands

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Abstract

Several questions pertaining to the marine communities at the Prince Edward Islands are addressed. Firstly, the nature of the 'island-mass effect', and the cause of the frequently recorded diatom blooms in the area are examined. It had been suggested that the cause of the blooms is related to the presence of a Taylor Column-induced, low density, stationary eddy which stabilises the water column. On a cruise in April/May 1989, temperature, salinity, nutrients, chlorophyll and primary production were measured at 90 stations in a large grid centred on the islands. These, together with data collected on previous cruises, are used to show that the repeated occurrence of diatom blooms was not a result of nutrient enhancement. No evidence for light-limitation of phytoplankton was found. The evidence and theoretical basis which was used to predict the existence of a Taylor Column is questioned. An alternative hypothesis for explaining the blooms is presented. It is argued that these local blooms are simply the result of seeding by a dormant stock of diatom resting spores from the shallow sediments around the islands. This hypothesis hinges on three observations: (1) the blooms occur only over shallow sediments and are not a feature of the open ocean, (2) the species *Chaetoceros radicans* has been responsible for the bloom each time the cells were identified, and (3) *C. radicans* forms a rapidly sinking, heavily silicified, resting spore.

A conceptual framework of how zooplankton lipid composition is affected by diet, latitude and seasonal feeding strategies is introduced as a means for ascertaining, by lipid assays, these aspects of the biology of sub-Antarctic zooplankton. The lipid content, class composition and fatty acid composition of 8 euphausiid and 2 copepod species were assayed. The lipid contents of the euphausiids were low for late summer compared to congeners from higher latitudes. The copepods were, however, richer in lipids. Surface chlorophyll-*a* in the sub-Antarctic is low when compared to the oceanic fronts to the north and south, suggesting that this region is not a productive feeding environment for zooplankton. Most species in this region occur here at the extreme of their known ranges. *Thysanoessa vicina, T. macrura.* and

Metridia spp. were found to contain wax esters in abundance, whereas *Euphausia* spp., *Nematoscelis megalops* and *T. gregaria* stored no wax ester. The fatty acid composition points to a herbivorous diet for all specimens examined, though it is likely that those lipid-poor species which do not store wax ester will switch to an alternative winter diet. Furthermore, the sub-tropical *Thysanoessa gregaria* and *Metridia lucens* contained little or less wax ester compared to their congeners of the Antarctic, which presumably reflects the different feeding strategies associated with latitudinal differences.

A description of the distribution of the recently described kelp, *Macrocystis laevis*, which occurs only at these islands, is presented. The standing stock is estimated from measurements taken on three occasions. Net production is estimated at 7.7 $gC.m^{-2}.d^{-1}$ and 11.5 $gC.m^{-2}.d^{-1}$ during the months of April and August respectively. Based on calculations for *M. laevis* and *Durvillea antarctica* (the two species making up most of the macrophyte biomass) macrophytes are more productive per unit area than the phytoplankton but contribute less to the seas around the Prince Edward Islands by virtue of their small spatial coverage. The contribution of *M. laevis* production to the nearshore ecology of the islands seems limited, as it is suspected that almost all of its production is exported to the open ocean pelagic system.

The patterns in the benthic community of the archipelago are described from an extensive qualitative survey at 57 stations. The benthos was sampled with an epi-benthic sled. In addition, underwater photographs were taken at most stations. Macrofaunal species diversity was found to be impoverished compared to Antarctic communities. This is ascribed to the extreme isolation and geological youth of the archipelago. A cluster-analysis based on species abundance alone aggregated most stations into 8 recognisable communities. Each of these communities had a unique depth and substratum combination. Indicator species are listed for each of the groups. Deep, rocky substrata were dominated by Porifera, bryozoans and cnidarians, while soft-substrata were dominated by polychaetes, bivalves and brachiopods. Errant forms cinsisted predominantly of echinoderms, with crustaceans being important in shallower habitats. Filter-feeders dominate the islands benthos. The shrimp *Nauticaris*

marionis was found to be abundant everywhere. The likely influence of the islands' oceanographic processes on the benthos is discussed.

The major findings are drawn together in terms of the trophic dynamics of the seas surrounding the islands. Proposed future research directions include: ocean current measurements, quantification of diatom resting spore densities and sinking fluxes, zooplankton abundance measurements, and quantification of the benthic biomass.

Contents

Introduction

Marion Island and Prince Edward Island, collectively known as the Prince Edward Islands, occur in the sub-Antarctic sector of the Indian Ocean (46°50'S, 37°50'E). Together they rise abruptly from the ocean floor at 3000 m to form a shallow plateau, referred to as an archipelago for convenience.

Since the first comprehensive monograph on the Prince Edward Islands, which covered aspects of its climatology, geology, biogeography and systematics, edited by E.M.Van Zinderen Bakker, J.M. Winterbottom and R.A. Dyer (1971), there has occurred a marked increase in scientific interest in these islands and adjacent waters. This started with a thorough examination of the systematics and ecology of the rocky intertidal community (De Villiers 1976). The voyage of the French vessel 'Marion Dufresne' in 1976, which called at the Prince Edward Islands, was an important initial expedition to describe the oceanographic environment. Subsequently, oceanographers and biologists gained access to the islands and adjacent waters on supply and relief cruises on the ships 'M.V. S.A. Agulhas' and 'R.S. Africana'. By 1988 notable advances had been made by oceanographers studying physical aspects of the water, plankton ecology and plankton systematics and biogeography. An extensive survey of the benthic fauna was near completion, while the feeding habits and behaviour of the resident marine mammals and avifauna had been intently studied. I intend to briefly introduce the specific points of interest relating to the marine environment of the Prince Edward Islands at the time, such that this work might be placed into some perspective.

The central theme, though one seldom expressed explicitly, towards which the marine scientific investigations were being directed was gaining knowledge on the principal sources of food sustaining the large biomass of avifauna in particular, but also the lesser known rich benthic community. Is the Prince Edward Island archipelago an oasis in an oceanographic desert? Various scientists were interested by specific problems, and several hypothesis had been, or could be, tested. I will discuss those which pertain to this work below, giving some treatment to the theory and rationale for each.

What is the physical effect of the interaction of the Antarctic Circumpolar Current (ACC) with the Prince Edward Island archipelago on the structure of the water-mass? From measurements taken in 1976 it was apparent that some kind of 'island-mass effect' left a signature in the chlorophyll distribution in the lee of the Prince Edward Islands and the Crozet Islands. The nature of this effect was unclear. Grindley and David (1985) proposed that upwelling in the lee of Marion Island would account for the surface distribution of temperature, salinity, nutrients and chlorophyll. Allanson et al. (1985) disputed this interpretation from current measurements in addition to measurements of temperature, salinity, nutrients and chlorophyll taken a few years later. They suggested, after some theoretical considerations, that a 'Von Karman Street' - a wake embedded with eddies - develops in the lee of the islands. In this train of eddies, nutrient-rich water would be sequestered to the surface. Perissinotto and Duncombe-Rae (1990) remained with the concept of eddies, but pointed out that a mechanism other than nutrient-enrichment was responsible for persistent phytoplankton blooms which recur in the lee of the islands and over the plateau. A more complex oceanographic feature was proposed, supported from a dimensional analysis and from physical data. A 'Taylor Column' - a disturbance of flow above a bump on the ocean floor - might force a stationary anticyclonic (warm core) eddy above the archipelago, and periodically shed a cyclonic (cold core) eddy downstream. Duncombe-Rae (1990) calculated that a stationary eddy would account for decreased salinity over the plateau by entrapping fresh-water runoff from the islands, and provided further support for the theory. The existence of a stationary eddy would hold appreciable consequences for the plankton community, in particular the phytoplankton.

What is the cause of recurrent phytoplankton blooms in the vicinity of the Prince Edward Islands? While this is a separate question from that raised in the previous paragraph, one being biological the other physical, the answer to either one should, in part at least, provide the answer to the other. This rationale meant that the two questions were rarely treated seperately. El Sayed et al. (1979) first reported the occurrence of a rich diatom bloom in the lee of the islands, whereas the oceanic water was poor in chlorophyll content. Scientists on subsequent cruises reported the same phenomenon. As described in the previous paragraph, hypotheses were erected and replaced, some from particular data sets (Grindley and David 1985; Allanson et al.

1985; Perissinotto et al. 1990) and others from general, theoretical considerations (Boden 1988; Perissinotto and Duncombe Rae 1990). Boden (1988) suggested how a disturbance in the current pattern might account for observed species distribution patterns. Perissinotto and Duncombe Rae (1990) used the 'Taylor Column' theory and algal physiological evidence to explain the 'island-mass effect'. An anticyclonic, warm core eddy traps buoyant water at the surface which increases the stability of the water column. To understand how a stable water column might favour phytoplankton growth, one should be familiar with the anomaly of (sub)-Antarctic water being simultaneously rich in nutrients but poor in chlorophyll. One explanation currently favoured is that high rates of surface-water turnover prevent a phytoplankton community from developing in the light-field, and from stripping nutrients (Holm-Hansen 1985). Phytoplankton in these waters are thus believed to be 'light-limited'. It can be appreciated that, should a stationary eddy exist, this would adequately explain the recurrent phytoplankton blooms.

Does the sub-Antarctic water-mass have an indigenous plankton community, or is it characterised by vagrant sub-tropical and Antarctic elements? The narrow band of sub-Antarctic water in the Indian ocean lacks clear definition. Sir Deacon (1983) suggested that this was a result of the ACC flowing over an irregular bottom topography. Boden (1988) found both sub-tropical and Antarctic phytoplankton at the Prince Edward Islands. Miller (1985) found a dissimilarity between zooplankton samples from the Prince Edward Islands and from Gough Island, on the Sub-tropical convergence, although most species occurred at both sites and no indicator species could be isoloated. Grindley and Lane (1979) noted a strong representation of Antarctic zoooplankton at Marion Island. Indeed, they used this as evidence for the possible upwelling of Antarctic water at the islands. Sub-Antarctic oceanic water is not rich in plankton. Nonetheless, sitting between two productive oceanic fronts, the avifauna at the Prince Edward Islands is in a position to overcome this apparent local food scarcity. Whether a sufficiently large herbivorous zooplankton community exists to make the locally rich diatom production available to sea-birds merits investigation. The gut contents from penguins and petrels from the islands do contain zooplankton which occur at the islands and at the fronts. As the foraging range of these birds could be enormous, there was little indication of where they

fed. Nigel Adams, of the Percy Fitz-Patrick Institute for African Ornithology (UCT), is currently addressing this issue.

Is the sub-Antarctic marine environment strongly seasonal? The bi-annual relief voyages which provide the only access to these islands have not allowed seasonal comparisons. Mid-summer and mid-winter extremes in production have not been measured. The day-length varies from 16 hours in December to 8 hours in June, which suggests that a strong seasonal pattern in production is likely. How will the herbivorous zooplankton species overcome a winter shortage of food? Two hypotheses present themselves: (1) herbivores store lipid from which they subsist during winter, and (2) herbivores switch to an alternative food source in winter. In the less seasonal Agulhas Bank water, 1000 miles to the north, herbivores have a life-history which corresponds to short-term fluctuations in food availability. Their breeding cycles are opportunistic and do not occur during specific seasons, whereas Antarctic herbivores spawn at regular times during the year.

Of what significance is the contribution of kelp to the economy of the island's marine communities? Notable features of the shallow waters around the islands are extensive forests of the kelp *Macrocystis laevis*, which was only very recently described and appears to be endemic to the Prince Edward Islands. Another species, *Durvillaea antarctica*, forms a continuous band at the intertidal zone around both islands. The presence of a shallow submarine shelf and a terrestrial environment provides a purchase for a rich benthic community and a large sea-bird community respectively. Is this convenience alone sufficient to explain their presence? The hypothesis to be tested was that the island-enriched production supports this large biomass. *Macrocystis*, known to be highly productive in other parts of the world, was identified as a likely major source of production which might form an integral part of the energy flow through the island's marine food webs.

In this thesis I address most of the above issues to some extent in four chapters, each dealing with a specific and quite different aspect of the marine ecosystem. Chapter I is a re-examination, based on some additional data collected on the second cruise of the 'Marion Offshore Ecological Survey' (MOES II) during April/May 1989, of the cause of the

phytoplankton blooms and the associated oceanographic processes. In this chapter, I propose a new explaination for the recurrent blooms of the diatom *Chaetoceros radicans* at the Prince Edward Islands. Chapter II concerns the lipid composition of several of the abundant zooplankton species in the area. A conceptual framework for the synthesis and storage of lipids as related to the mode of feeding is introduced as a possible technique for understanding some of the basic feeding strategies of the zooplankton of the sub-Antarctic, and to tie this to aspects of their ecology. The questions dealing with seasonality and biogeography are touched upon in this chapter. In chapter III, I describe and quantify the standing stocks, growth and production of *Macrocystis laevis*, and estimate its relative importance to the marine food webs of the archipelago. Chapter IV provides a descriptive account of the patterns in the benthic communities based on statistical analyses of a large data set of species-abundance and physical variables sampled at 57 sites on the island plateau. Finally, in a brief conclusion the principal findings of this thesis are drawn together

Chapter 1

The role of diatom resting spores in a sub-Antarctic island-mass effect

Abstract-Massive diatom blooms dominated by *Chaetoceros radicans* have been often recorded over the Prince Edward Island plateau, but never at adjacent open ocean stations. Several hypotheses have been advanced to explain this 'island-mass effect, the latest being that a low density core eddy over the plateau traps low salinity water, and possibly reduced nitrogen from the islands, to create a shallower mixed depth and a favourable light environment for phytoplankton growth in otherwise unstable water. Physical, chemical and production measurements were taken on an extensive sampling grid around the Prince Edward Islands during April 1989 to test this hypothesis. In contrast to previous cruises (March 1976, April 1982, April and November 1983, April 1987), no phytoplankton bloom was observed during the 1989 survey. Chlorophyll-*a* concentrations were low (< 0.5 mg Chl-*a* m^{-3}) and dominated by pico-planktonic cells. At all stations, nutrient concentrations were high. Although the high chlorophyll concentrations recorded on previous cruises depleted nutrients, blooms evidently were not stimulated by an input of nutrient-rich water. Direct evidence for light-limitation was absent. The oceanographic evidence for a stationary low density core eddy at these islands is scant and open to alternative explanations. The theoretical basis for predicting an anticyclonic low density eddy at the Prince Edward Islands by a Taylor column mechanism is unfounded since: (1) it is unclear whether a low or a high density eddy is to be expected above the feature, (2) the horizontal scales typical of the Prince Edward Islands environment are far smaller than those used in theoretical predictions, and (3) the archipelago is 93% of the height of the water column and surfaces in places, whereas Taylor columns are predicted for shallow topographic features. The repeated positioning of the bloom at this and other sub-Antarctic islands could be explained as a seeding phenomenon. *Chaetoceros radicans* has been responsible for the inter-island

blooms in March 1976, May 1983, November 1983 and April/May 1987. *Chaetoceros radicans* forms a heavily silicified spore. I will provide arguments which suggest that the chlorophyll maxima observed over the archipelago are due to seeding of *Chaetoceros radicans* from shallow sediments.

Introduction

The Prince Edward archipelago (46°50'S, 37°50'E) consists of two volcanic islands which outcrop from a relatively shallow submarine plateau in the sub-Antarctic, south of the Subtropical Front (STF), but north of the Antarctic Polar Front (APF) (figure 1). Phytoplankton blooms have often been encountered in the inter-island region and over the island plateau, whereas chlorophyll concentrations in the adjacent open ocean is persistently low. El-Sayed et al. (1979a) recorded a bloom of the diatom *Chaetoceros radicans* in March 1976 to the east of the islands. Parker (1984) gave details of local chlorophyll maxima between the islands recorded during April 1982, May 1983 and November 1983. On the November 1983 voyage of the 'M.V. S.A. Agulhas', Boden (1988) recognised two blooms, one of *C. radicans*, the other of the Antarctic silicoflagellate *Dictyocha speculum*, in spatially distinct patches around Marion and Prince Edward Islands. Cell counts were in the order of 10^9 cells.m^{-3} (> 2 mg Chl-*a* m^{-3}, with production up to 190 mg C m^{-2} h^{-1}), forming dense mats which obscured other species under microscopy. Again, in 1987, Boden (1988) reported a similar bloom of *C. radicans*, but noted that away from the islands this species was absent, where counts of other species were in the range of 10^3 to 10^4 cells.m^{-3}.

Plancke (1977) and El-Sayed et al. (1979a,b) found high chlorophyll concentrations in the lee of the Crozet Islands and the Kerguelen-Heard plateau, in addition to the Prince Edward Islands, and deduced that production was influenced by an 'island-mass effect". The complex nature of this effect Plancke (1977) ascribed to a system of upwelling, while El-Sayed et al. (1979a,b) prefered not to advance an explanation on the mechanism of the effect until more data were available. Deacon (1983) concluded that there is more interchange and less clear gradation between Antarctic and sub-Antarctic waters in the vicinity of Marion, Crozet, Kerguelen and Heard Islands (40-70°E) than in most longitudes. The irregular bottom topography of this region, together with the Antarctic Circumpolar Current, is expected to cause such complex features as eddies, wakes and Taylor columns.

Several explanations have been advanced to explain the observed elevation of chlorophyll in the Prince Edward Island waters. Allanson et al. (1985) hypothesised that the shallow oblique plateau, on which the Prince Edward Islands rest, interacts with the west

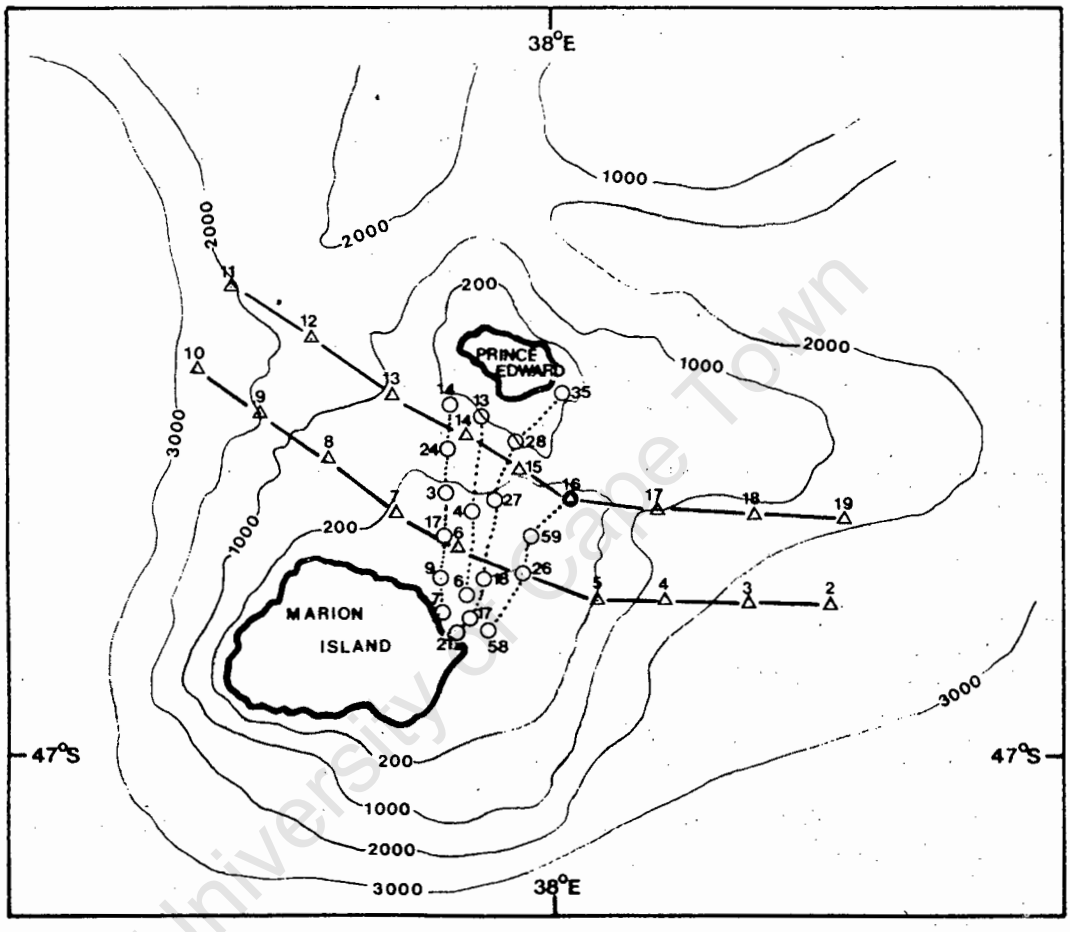

Figure 1: The Prince Edward Island plateau. Isobath measurements are in meters. The transect lines refere to data presented in figure 9 and 10. The four north-south transects, with stations represented by open circles, were undertaken in March 1976, May 1983, March 1984 and May 1987, the two east-west transects represented by open triangles were undertaken in April/May 1987 (from Perissinotto & Duncombe Rae 1990).

wind drift so as to set up a vortex field (a wake characterised by contra-rotatating eddies) in the lee of the archipelago. In these eddies nutrient sequestration into surface waters might be enhanced. Perissinotto et al. (1990) pointed out that the extraordinarily high surface nutrient concentrations in the sub-Antarctic could not be limiting phytoplankton growth, and ascribed the recurrent blooms to increased stability and shallower mixing in the inter-island region. Indeed, light limitation has been a recurrent theme as an explanation for the low rates of primary production generally observed in the southern ocean (Holm-Hansen 1985; Priddle et al. 1986).

The mechanism for increased stabilization at the islands was suggested to be due to the presence of a stationary low density core eddy analagous to a Taylor column, and the retainment of freshwater runoff from the islands in the eddy (Perissinotto and Duncombe Rae 1990). The Prince Edward Islands receive in excess of 2000 mm precipitation annually. Duncombe Rae (1989a) calculated that the quantity of freshwater drained from Marion Island over a 20 day period could account for the surface salinity minimum observed during April/May 1987, assuming the existence of an eddy with a water retention time of this order.

As part of the Marion Island Off-shore Ecosystem Study (MOES II), the track of the 'M.V. S.A. Agulhas' during April-May 1989 was planned to test these hypotheses. Eighty-nine stations were occupied, arranged along grid lines extending 600 km east and west and 300 km north and south of the islands, with greater resolution near the island plateau (figure 2). Measurements included CTD, XBT, nutrient and chlorophyll analyses, continuous light recordings and post size-fractionated ^{14}C incubations. The MOES II cruise is the ninth collection of bio-oceanographic data from this region; the dates of the previous cruises were March 1976 ('R.V. Marion Dufresne'), April 1982 ('M.V. S.A. Agulhas'), September 1982 ('R.S. Africana'), May 1983 ('M.V. S.A. Agulhas'), March 1984 ('M.V. S.A. Agulhas') April/May 1985 ('M.V. S.A. Agulhas'), April/May 1986 ('M.V. S.A. Agulhas') and April/May 1987 ('M.V. S.A. Agulhas'). The Prince Edward Islands have received considerable interest from oceanographers, this paper being the fifteenth in a decade to report on phytoplankton and related matters following Grindley (1978), El-Sayed et al. (1979a,b), Grindley and Lane (1979), Parker (1984), Miller et al. (1984), Allanson et al. (1985),

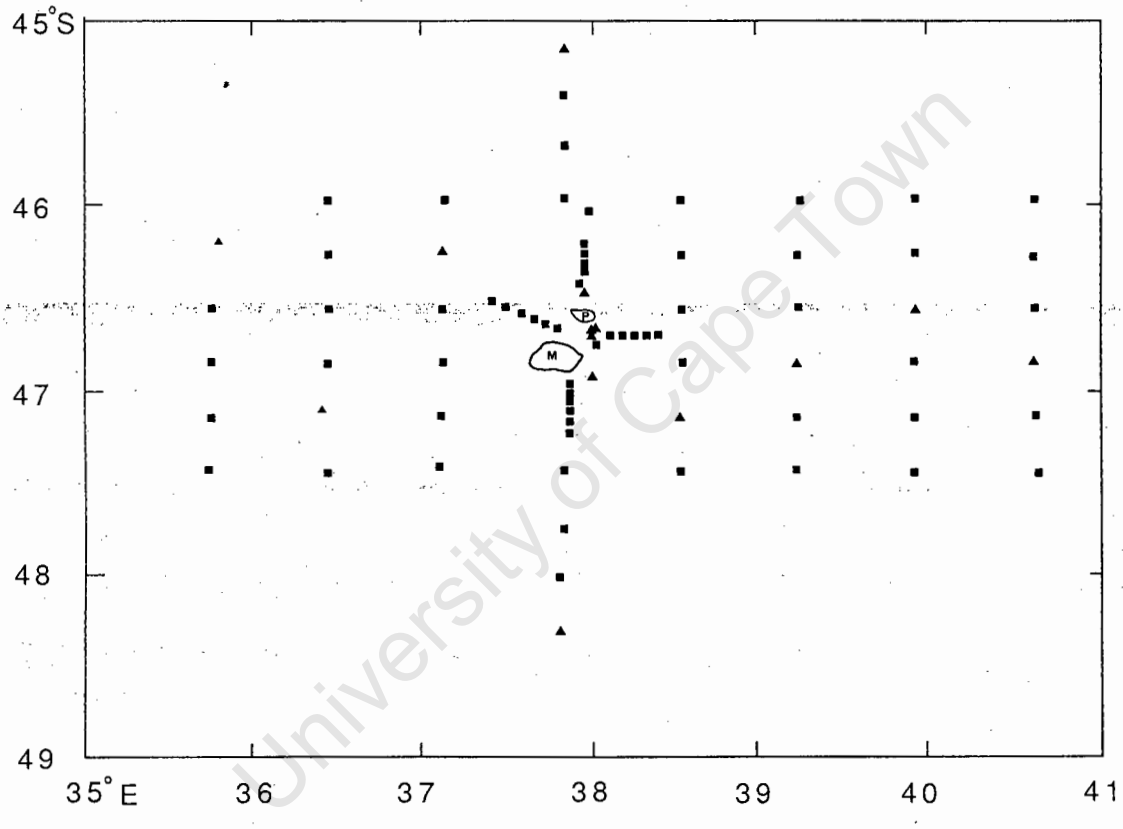

Figure 2: The position of stations occupied during April/May 1989. At all these stations CTD measurements, nutrient measurements, and chlorophyll-a measurements were undertaken. At stations denoted by triangles ^{14}C incubations were done.

Grindley and David (1985), Boden and Parker (1986), Boden (1988), Duncombe Rae (1989a), Perissinotto and Boden (1989), Perissinotto et al. (1990) and Perissinotto and Duncombe Rae (1990). The present work draws on nutrient and physical data, chlorophyll distribution and primary production rates recorded on the April/May 1989 and previous cruises to discuss the most likely cause of blooms around these islands.

Methods

The methods used on cruises prior to 1989 are reported elsewhere; viz. El-Sayed et al. (1979a,b) [March 1976], Parker (1984) [April 1982, September 1982, May 1983, November 1983, March 1984], Perissinotto and Boden (1989) [April/May 1985 and 1986], Duncombe Rae (1989b) [this latter publication includes a full listing of the data collected during April/May 1987], while the methods employed during 1989 are reported below, and those pertaining to the collection of physical and chemical data can be found in Van Ballegooyen et al. (1989) which includes a full listing of the data.

Water samples were drawn from five depths at which the irradiance corresponded to 100, 75, 50, 30 10 or 1% of surface irradiance. The light extinction coefficient was determined by submerged light measurements. Water samples were collected with 5-l PVC Niskin bottles and transferred to the laboratory in plastic buckets shaded in black plastic bags.

Chlorophyll concentrations at depths within the euphotic zone were determined from sea-water fractionated into three size classes, viz (1) < 200 µm (mesh filter), (2) < 15 µm (mesh filter), and (3) < 2 µm (Nuclepore filter). The fluorescence of the samples was measured in vivo and this value converted to chlorophyll-*a* concentration from the equation,

$$\text{mg Chl-}a\ \text{m}^{-3} = 0.024\ (\text{fluorescence}) - 0.039, \qquad (1)$$

which was calibrated from standard chlorophyll extractions.

The rate of primary production was measured using the ^{14}C technique of Steenman Nielsen (1952), as modified by Strickland and Parsons (1972). Three replicate 300 ml light samples and one 300 ml dark sample were innoculated with 20 - 25 µCi of $NaH^{14}CO_3$. The bottles were incubated on deck at sea surface temperatures and shaded with precalibrated

shade cloth which was tested for its capacity to exclude light. Light intensities were recorded throughout the day on deck at two-minute intervals with a Dirmkirn Star Pyronometer. Incubations lasted for four-and-a-half daylight hours, after which the bottles were retrieved and shaded in black plastic bags. The incubated samples were fractionated into the three size classes described earlier, using 200 µm and 15 µm mesh filters and 2 µm Nuclepore filters. Phytoplankton was finally filtered onto Whatman GF/F filters and rinsed three times with 0.2 µm filtered sea-water. Filters were placed in liquid scintillation vials, to which 10 ml of the scintillation cocktail Insta-gel (Packard Instrument International) was added. Radio-activity was measured on-board using a Beckman Scintillation counter, and corrected for the counting efficiency as determined by external standardisation. The precise ^{14}C activity of the added $NaH^{14}CO_3$ was determined for each experiment.

Water column stability (E) was estimated as the ratio of the buoyancy (upward acceleration) of a water parcel to gravitional acceleration:

$$E = -a_z / g. \quad (2)$$

E is measured in m^{-1}, a_z is the upward acceleration per unit of length dz, 10 m in this case (units, s^{-2}), and g is the acceleration due to gravity (units, m s^{-2}). From equation 17 of Millard et al. (1970), not repeated here because of its complexity, N^2 was computed, where N is the Brunt-Vaissala frequency, the natural period of oscillation for a water parcel displaced adiabatically from its rest position (units, s^{-1}). E was calculated from the relation:

$$E = N^2 / g \quad (3) \text{ (Millard et al. 1990).}$$

The depth of the upper mixed layer was estimated to extend to the depth at which the potential density changed by 0.03 kg m^{-3} within 10 m, although often this criterion was satisfied several times within the water column. Always the first density change exceeding this value was taken to be the depth of mixing (Z_m).

Results

The data used in the analyses to be presented are too extensive to list, but appear in two published volumes: Duncombe Rae 1989b and Van Ballegooyen et al. 1989. The surface chlorophyll distributions around the Prince Edward Islands during April 1987 and 1989 are

presented in figures 3 and 4 respectively. The mean and standard deviation of the surface temperature, and of the concentrations of NO_3, NO_2, NH_4, Urea, PO_4 and SiO_2 during these cruises are listed in table 1 to provide an indication of how rich the sub-Antarctic water is in the major inorganic nutrients. In order to check for relationships between the spatial distributions of the nutrients, physical variables and chlorophyll-a, linear regression analyses were applied to a series of paried variables. The results of these regressions for the 1987 and 1989 data are listed in table 2.

During the 1987 cruise the pico-plankton (< 2μm), nano-plankton (2-20 μm) and net-plankton (> 20 μm) size fractions accounted for < 3% ($p < 0.1$), 40% ($p < 0.01$) and 99% ($p < 0.001$) of the variation of primary production. During April/May 1989 ($p > 0.05$), the trend was reversed; on average, the pico-plankton accounted for > 60% of the surface chlorophyll-*a* and was the only size fraction to explain variation in total chlorophyll-*a* concentration ($p < 0.005$). The pico-phytoplankton concentrations during this cruise were ubiquitous, ranging between 0.05 and 0.35 mg Chl-*a* m^{-3} within the upper mixed layer.

P^B_m ratios (the maximum hourly production rate normalised by chlorophyll-*a* concentration, for each station) ranged between between 0.47 and 14.59 mg C h^{-1} (mg Chl-a)$^{-1}$ during 1987 and between 0.56 and 4.29 mg C h^{-1} (mg Chl-a)$^{-1}$ during 1989. The light intensity which yields P^B_m (I_K) was not calculated as the product of P^B_m and the slope of the P-I curve (recommended by Platt and Jassby 1976), since observations from only five depths provided little confidence in the parameters of the fitted P-I curve. Instead, a more robust but less precise method was used by equating I_K to the light intensity at whichever of the five depths yielded P^B_m. I_K values calculated from the 1987 and 1989 data were similar, averaging at 1924 mmol PAR.h^{-1}, where the incident surface radiation averaged at 2436 mmol PAR.h^{-1}. The results of correlations of P^B_m and I_K against the mixed layer depth, mean water column stability integrated over 100 m and reduced nitrogen concentrations are given in table 3.

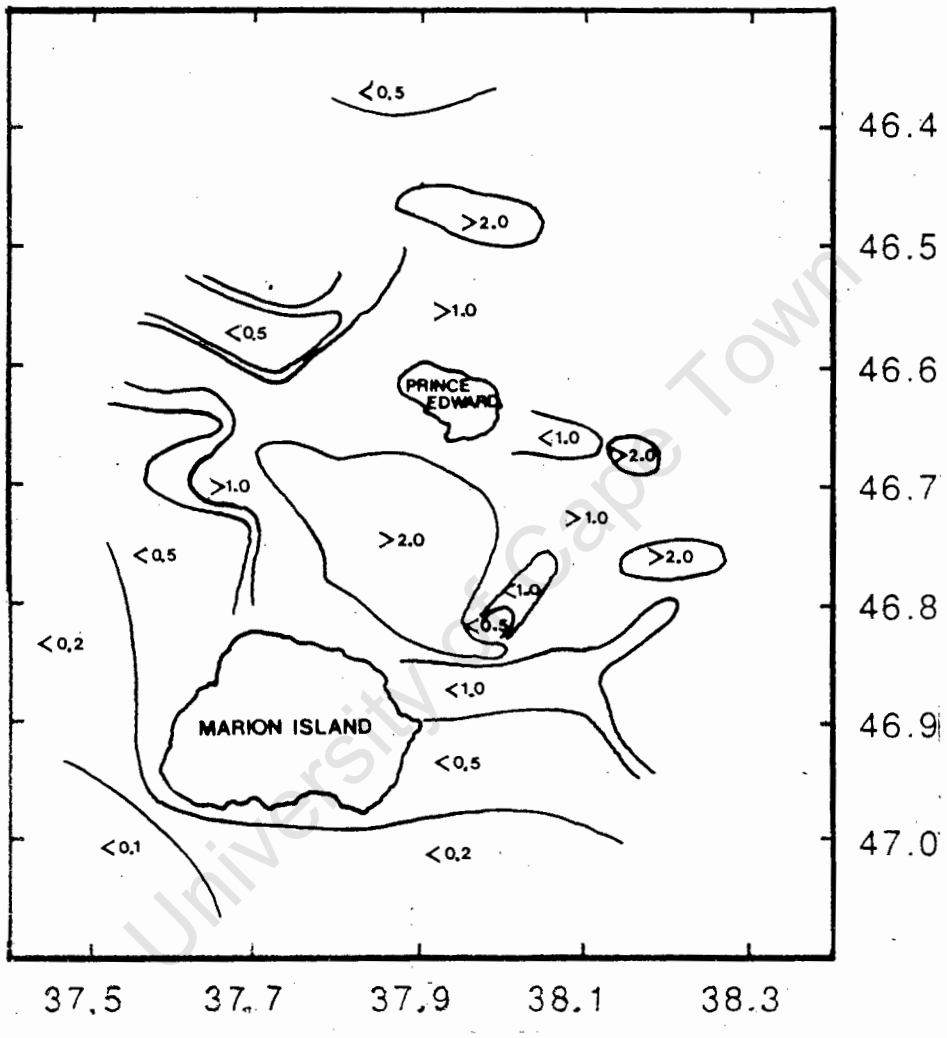

Figure 3: Suface Chlorophyll-a distributions during April/May 1987. Units are mg Chl-a m^{-3}.

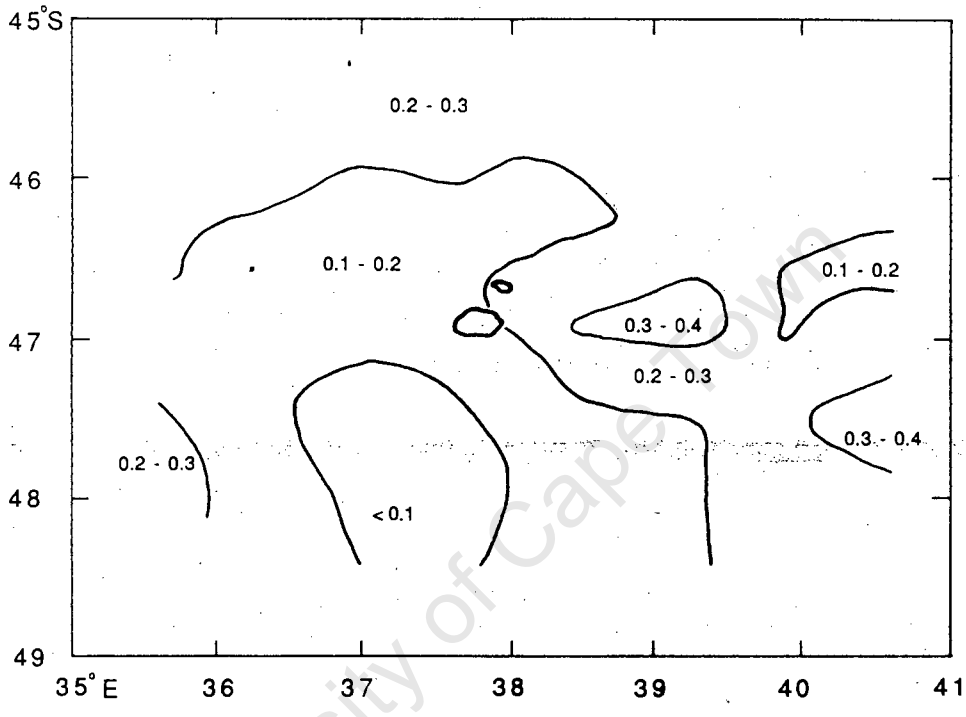

Figure 4: Suface Chlorophyll-*a* distributions during April/May 1989. Units are mg Chl-*a* m^{-3}.

Table 1: The means and standard deviations of suface temperature, salinity, and major nutrient concentrations measured at the Prince Edward Islands during the MOES I (April/May 1987) and MOES II (April/May 1989) cruises.

	Temperature °C	Salinity psu	NO_3 mmol m^{-3}	UREA mmol m^{-3}	NH_4 mmol m^{-3}	PO_4 mmol m^{-3}	SiO_2 mmol m^{-3}
MOES I							
Mean	5.963	31.154	16.048			0.843	1.284
SD	2.021	9.121	4.509			1.066	1.128
MOES II							
Mean	6.367	32.526	19.248	0.778	0.307	1.613	3.017
SD	1.078	5.274	4.726	0.315	0.210	0.463	1.119

Table 2: Results of regression analyses between surface chlorophyll-a, and physical and nutrient measurements. Data were fitted to a linear model, $y = a + b\,x$. Slopes are given where there is greater than 95% confidence in the relationship.

	Dependant variable	Independant variable	r^2	p	Slope
MOES I	Chl-*a* concentration	Latitude	0.13	0.041	-2.30
April/May	Chl-*a* concentration	Temperature	0.01	0.531	
1987	Chl-*a* concentration	NO_3	0.00	0.770	
	Chl-*a* concentration	SiO_2	0.39	0.000	-0.43
	Chl-*a* concentration	PO_4	0.09	0.105	
	Stability within 50m	Surface salinity	0.02	0.486	
	Stability within 75m	Surface salinity	0.02	0.492	
	Stability within 100m	Surface salinity	0.02	0.503	
MOES II	Chl-*a* concentration	Latitude	0.05	0.512	
April/May	Chl-*a* concentration	Temperature	0.15	0.000	0.041
1989	Chl-*a* concentration	NO_3	0.04	0.056	
	ln(Chl-*a* concentration)	NH_4	0.27	0.000	-0.121
	Chl-*a* concentration	UREA	0.00	0.734	
	Chl-*a* concentration	SiO_2	0.02	0.245	
	Chl-*a* concentration	PO_4	0.00	0.679	
	Stability within 50m	Surface salinity	0.00	0.845	
	Stability within 75m	Surface salinity	0.00	0.877	
	Stability within 100m	Surface salinity	0.02	0.254	

Table 3: Results of regression analyses between maximum photosynthetic capacity (P^B_m) and average water column stability integrated over the upper 100 m (E) and the depth of the upper mixed layer (Z_m), and between the light level which yields $P^B_m(I_K)$ and water column stability and the depth of the upper mixed layer, for data collected in 1987 and 1989. Data were fitted to a linear model, $y = a + b\,x$. The sign of the slope is given if $p < 0.2$.

	Dependant variable	Independant variable	r^2	p	Slope
MOES I	P^B_m	E	0.08	0.47	
April/May	P^B_m	Z_m	0.00	0.83	
1987	I_K	E	0.66	0.01	-
	I_K	Z_m	0.00	0.83	
MOES II	P^B_m	E	0.04	0.51	
April/May	P^B_m	Z_m	0.00	0.79	
1989	P^B_m	NH_4	0.07	0.38	
	P^B_m	Urea	0.20	0.15	-
	I_K	E	0.01	0.78	
	I_K	Z_m	0.01	0.75	

Discussion

Sub-Antarctic water shares with Antarctic water the anomaly of being simultaneously rich in nutrients but poor in chlorophyll. Nitrate, phosphate and silicate concentrations for the sub-Antarctic are typically 15-25 mg m^{-3}, 0.5-2.0 mg m^{-3}, and 1-4 mg m^{-3} respectively (table 1, Allanson et al. 1981). The low productivity of this region is well illustrated by a synthesis of underway surface chlorophyll-*a* measurements taken on 11 cruises by Japanese vessels from Freemantle, Australia, south-west across the Indian Ocean to SYOWA (69°20'S; 39°35'E) and on the return voyages north-west to Cape Town during early- and mid-summer respectively (figure 5). The 1.5° running mean (i.e. each data point is the mean of the chlorophyll-*a* determined within 0.75° latitude of that point) between the STF and the APF is low (0.2 - 0.3 mg Chl-*a* m^{-3}) and invariant (SD = ~ 0.1 mg Chl-*a* m^{-3}). The higher chlorophyll-*a* concentrations at the ice-edge is due to the stabilising effect of ice-melt fresh water, whereas higher chlorophyll-*a* concentrations at the APF in early summer and STF south of Africa are more than likely an expression of the strong frontal activity in this region. Lutjeharms et al. (1985) have discussed some of the likely causes of higher production at the front. These include (1) inclined isopycnals at the front leading to greater water column stability and (2) the development of cross-frontal eddies which introduce either nutrients or a thermally stratified surface layer across the front.

The Japanese results confirm observations made on French expeditions that the incidence of high chlorophyll concentrations (> 1.0 mg.Chl-*a* m^{-3}) in the sub-Antarctic (between 40° and 50°S) is island related (Plancke 1977, El-Sayed et al. 1979a, Treguer 1985), and is not a feature of the open ocean. The occurrence of massive diatom blooms observed on five cruises to the Prince Edward Islands (March 1976, April 1982, May 1983, November 1983 and May 1987) have been attributed to an 'island-mass effect' (El-Sayed et al. 1979a, Allanson et al. 1985, Boden 1988), as have the blooms recorded at Crozet, Kerguelen and Heard Islands in the sub-Antarctic Indian Ocean (El-Sayed and Jitts 1973; Plancke 1977; El-Sayed et al. 1979 a, b; Jacques et al. 1982; Tregruer 1985). The mechanism of this 'island-mass effect' is the subject of the ensuing discussion.

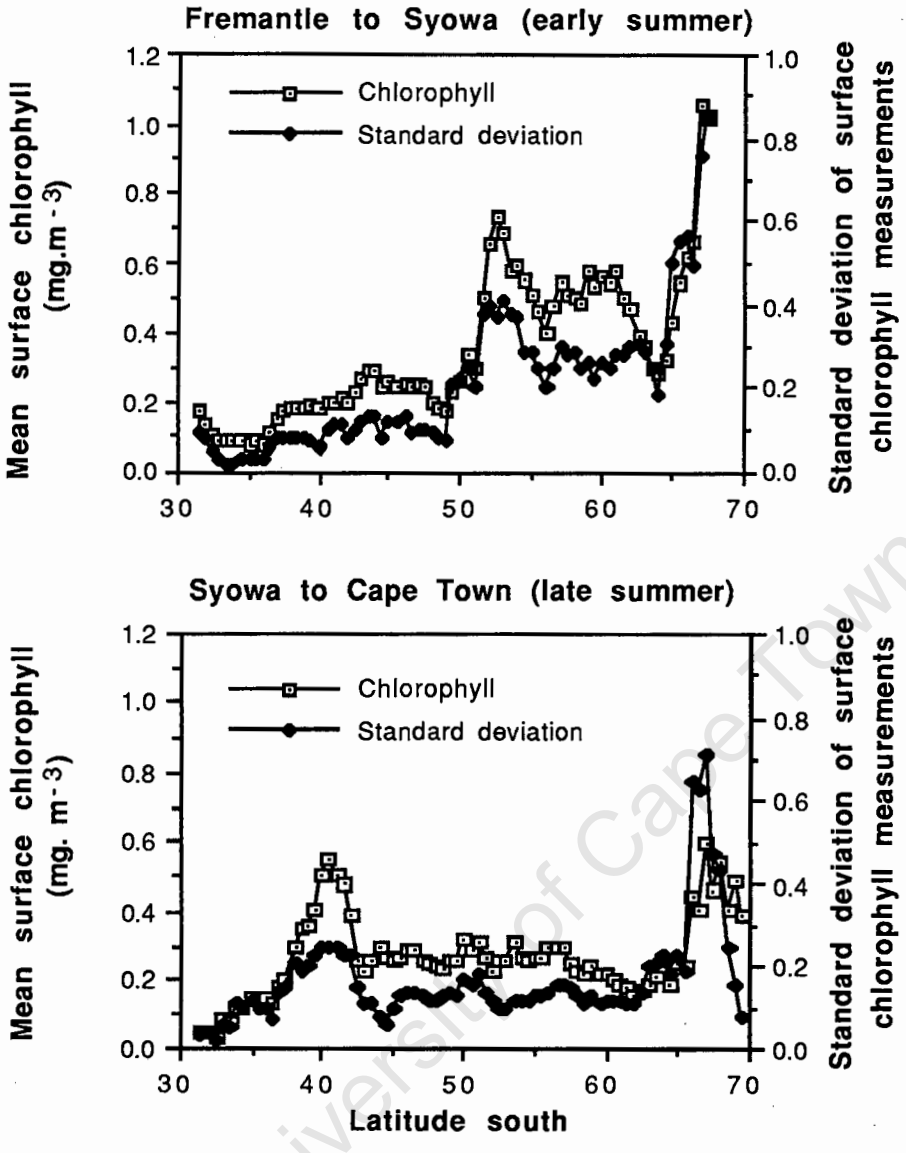

Figure 5: A synthesis of surface chlorophyll-a measurements taken on 11 cruises from Fremantle to Syowa (68°22'S; 44°08'E) in the months December and January, and again from Syowa to Cape Town in the months February and March. The data points are means for each half degree, but smoothed with a running mean spanning 1.5°. Data comes from Tominaga (1971), Nishiwaki (1972), Hoshino (1974), Ohyama and Mayama (1976), Ohno (1976), Fukuchi (1977), Kuroda (1978), Tanimura (1981), Yamagata and Fukui (1981), Fukuchi and Tamura (1982) and Watanabe and Nakajima (1983).

Nutrient enhancement

The absence of a correlation between chlorophyll-*a* concentration and either nitrate or phosphate during April/May 1987 and 1989 suggests that these major nutrients are non-limiting. Throughout April/May 1989 chlorophyll-*a* did not exceed 0.5 mg Chl-*a* m^{-3}, despite high nitrate and phosphate concentrations. Parker (1984), however, did find a negative correlation between chlorophyll-*a* and nitrate concentration ($p < 0.002$, $r^2 = 0.19$) and between chlorophyll-*a* and phosphate concentration ($p < 0.001$, $r^2 = 0.54$) for data pooled from March 1976, April 1982, September 1982 and May 1983. When chlorophyll concentrations are high, a depletion of nitrate and phosphate is evident. Similarly, a negative correlation between chlorophyll-*a* and silicate for the March 1976, April 1982, September 1982 and May 1983 data sets combined ($p < 0.001$; $r^2 = 0.30$) and for April/May 1987 ($p < 0.001$; $r^2 = 0.39$) implies that this nutrient can be limiting, although no correlation between chlorophyll-*a* and silicate for April/May 1989, when chlorophyll was low and silicate high at every station, implies that blooms are not induced by an elevation of silicate levels. From this evidence I conclude that the mechanism of the 'island-mass effect' is not a sequestration of deep, nutrient-rich water by either mixing, upwelling or advection processes.

When the reduced forms of nitrogen, ammonia and urea, were measured, negative correlations were obtained between these and chlorophyll-*a* (NH_4 vs Chl-*a*, April 1983, Perissinotto and Duncombe Rae 1990; NH_4 vs Chl-*a* and urea vs Chl-*a*, May 1987; NH_4 vs Chl-a, April 1989, table 2), even for the 1989 data with low chlorophyll concentrations. Generally, the negative correlation between the f-ratio (NO_3 uptake : total N uptake) and NH_4 concentration observed in the southern ocean (Olson 1980) is a result of preferential uptake of nitrogen in its reduced form (Probyn and Painting 1985). Thus during high N uptake NH_4 is depleted rapidly, resulting in a negative correlation with chlorophyll. On the 1989 cruise, stations with high NH_4 (> 0.7 mmol m^{-3}) and urea (> 1.0 mmol m^{-3}) concentrations (see averages in table 1) were not associated with high chlorophyll concentrations. An alternative, potentially significant source of reduced nitrogen is urea, which reaches very high concentrations close inshore adjacent to massive sea-bird colonies,

and may contribute up to 20% of total nitrogen uptake by phytoplankton in near-shore waters (Lucas and Probyn, in prep.). The surface distribution of NH_4 during 1987 suggests that its influence is very local, not extending to the centre of the inter-island region.

Light-limitation considered

Perissinotto et al. (1990) have argued that the incidence of high chlorophyll concentrations at the Prince Edward Islands is attributable to the stabilising effect of low-salinity water trapped in an eddy over the island plateau. At the Prince Edward Islands no correlation between chlorophyll concentration and sigma-t, stability, or the depth of the upper mixed layer has yet been found, either for the 1987 and 1989 data (table 2), or for data collected previously (Parker 1984). The absence of such correlations does, however, not negate the causal role that water column stability and mixing might play in regulating primary production, as the daily variation in these parameters is high and is unlikely to be matched by the response-time of the phytoplankton population in these cold waters.

The effect of unstable water and deep mixing is to decrease the average insolation of cells, and so light-limit the photosynthetic pathway. If production is light-limited, some indicator of photo-adaptation should correlate with the time that the phytoplankton spend in the light field. The maximum photosynthetic rate normalised by chlorophyll-*a* (P^B_m), or the light intensity (I_k) which yields P^B_m are measurable indices of photo-adaptation (Yentsch and Lee 1966, Prezelin 1981, Beardall and Morris 1981). The proportion of time spent in the light field (or the average insolation of phytoplankton) can be approximated, very roughly, by the depth of the upper mixed layer or water column stability within 100 m of the surface. Neither of these physical variables explained any variation of the physiological parameters P^B_m and I_k. A noticable exception here is the negative correlation between I_k and stability during 1989 ($p < 0.01$, $r^2 = 0.66$). I have no way of explaining this statistic, other than to ignore it as a *Type II error*, as a positive correlation was expected.

The use of physiological parameters as an index of photo-adaption in the wild is confounded by the natural assemblage of phytoplankton which spans two orders of magnitude in size, and eight in mass. As P^B rates are size dependent, variation in the

physiological parameters between natural phytoplankton assemblages can largely be accounted for by the size-structure of the communities, apart from adaptive changes of the photosynthetic mechanism (Harris 1986). Moreover, different species and sizes of phytoplankton, each adapted to, and selected by, a unique set of physical conditions, should collectively present a conservative physiological response to environmental change by altering the species-structure, and so mask the effect of substantial changes in the light history. Either (1) through error in the measurement of carbon uptake, or (2) through the inappropriate use of physiological and oceanographic indices or (3) as a true reflection of the algal physiology, direct evidence for light-limitation of phytoplankton growth at the Prince Edward Islands is not forthcoming, despite adequate measurements taken on several cruises. By this I do not imply that phytoplankton in the sub-Antarctic is not light-limited. On the contrary, light-limitation appears to be the most likely explanation for the low chlorophyll concentrations in the sub-Antarctic ocean, given that these waters are unstable. I do, however, imply that the variations measured in chlorophyll concentrations, photosynthetic rates and other physiological parameters, particularly those associated with diatom blooms at the Prince Edward Islands, is not accounted for by the light environment.

Size-structure variations

The size-structure of the phytoplankton community at the Prince Edward Islands seems to indicate that the 'island-mass effect' is operating principally on cells larger than 2 μm. Contrasting the bloom and non-bloom situations of 1987 and 1989 respectively, the net-plankton (> 20 μm), nano-plankton (2 - 20 μm) and pico-plankton (< 2 μm) size fractions were found to account for 99%, 40% and 3% of the variation of primary production during 1987. During 1989, only the pico-plankton size fraction accounted for chlorophyll-*a* variation ($r^2 = 0.50$). Pico-plankton chlorophyll-*a* in the sub-Antarctic is typically between 0.05 and 0.4 mg Chl-*a* m^{-3}.

I suggest that the size-structure difference between the 1987 and 1989 phytoplankton communities accounts a conspicuous discrepency between these data sets. Silicate was negatively correlated with chlorophyll-*a* during 1987, as this nutrient was depleted by

diatoms, but not during 1989. Another difference is that temperature explained 15% of the variation of chlorophyll-*a* measured in 1989 but did not correlate with that of 1987. This difference is accounted for by the massive localised diatom bloom in 1987 which was not induced by temperature effects. The more subtle variation in pico-plankton chlorophyll-*a* measured over a large latitudinal range during 1989 was partially explained by temperature, the mechanism possibly being temperature-controlled growth rates. The positive correlation between chlorophyll-*a* and temperature reported by Parker (1984) for data pooled from four cruises between 1976 and 1983 ($p < 0.001$, $r^2 = 0.62$) is difficult to interpret since his analysis includes 239 data points, 77 of which were collected at stations which he mapped, the remainder being collected underway at undisclosed localities.

Evidence for island-associated eddies

A considerable effort has been expended in searching for evidence for an island-trapped eddy which might explain the consistent loction of phytoplankton blooms over the shallow island plateau. Direct evidence for island-associated eddies is scant and theoretical considerations are frequently pursued. Here I briefly review the evidence and theory available in an effort to reach a conclusion on the island-associated eddies and how these might retain phytoplankton and enhance their productivity through the control of water column stability.

Allanson et al. (1985), on the basis of finding a circumferential arrangement of surface isopycnals in the lee of Marion Island in November 1983 (figure 6) deduced that the currents (which would flow parallel to the isopycnals through a geostrophic effect) would thus form an eddy. On the November 1983 cruise a series of semi-synoptic readings of current velocity and direction were taken at 5 m intervals to a depth of 50 m (Parker 1984). Allanson et al. (1985) noted that the readings at 25 m depth were in closest agreement with that predicated by the isopycnals. The direction of flow in a low density core eddy is anticyclonic (anticlockwise in the southern hemisphere). Four of the 25 m depth current meter readings (reproduced on figure 6) followed the isopycnals in an anticyclonic direction, and only one of these differed in direction (by more than 30°) from the surface measurement, where wind stress would play a major role. Although the average wind speed was 37 km

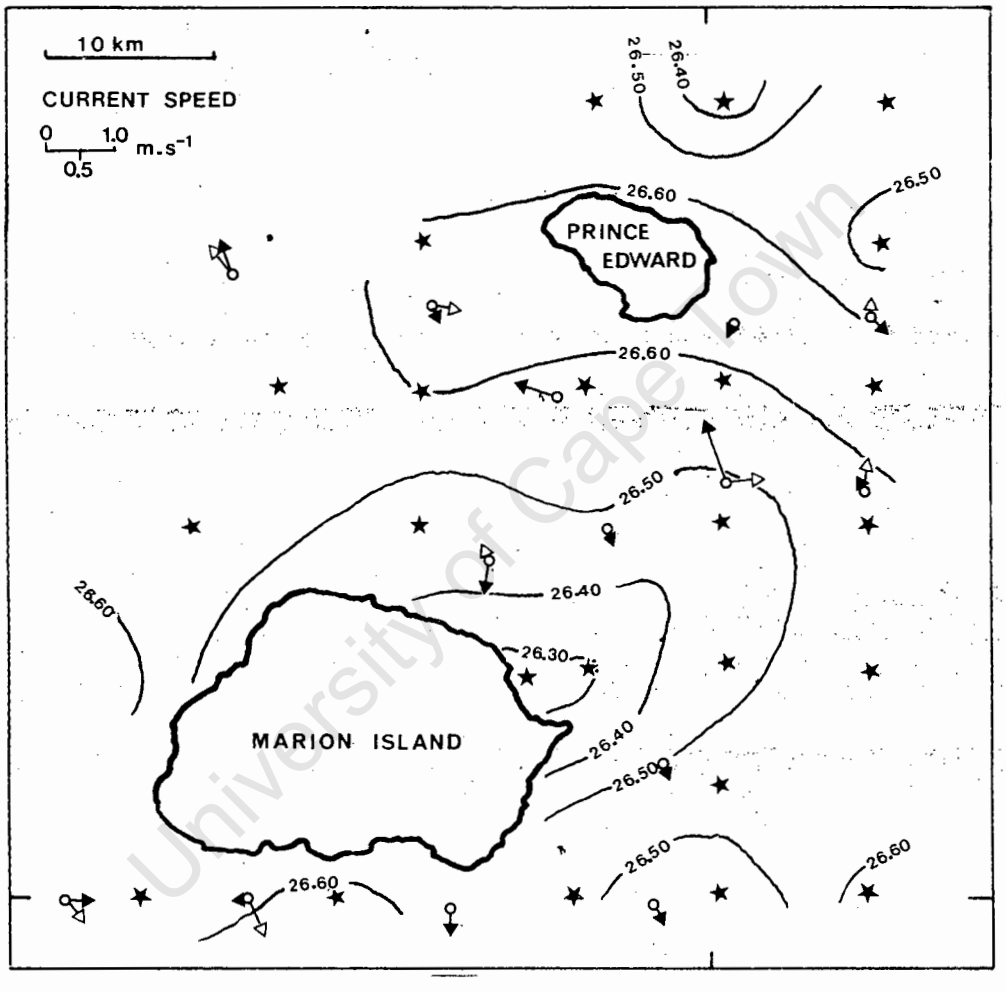

Figure 6: Contoured surface values of Sigma-t around the Prince Edward Islands in May 1983. Current speed and direction measured at two depths are presented: open arrow heads are surface readings, closed arrow heads are readings at 25 m depth. Drawing adapted from Allanson et al. (1985).

h^{-1} from the north-west, daily wind vectors were not compared with current speeds. Since the influence of wind on these currents is uncertain and the deeper measurements did not comply with the isopycnal predictions, this evidence for the eddy is not convincing. These authors suggested '*as an initial hypothesis that, where wind shear is of sufficient magnitude, and when coupled with the effects of the island on the structure of the west wind drift, it causes vortex fields to be set up in the lee of Marion Island.*'

The interaction of the Prince Edward Island archipelago with the fast flowing Antarctic Circumpolar Current (ACC) does create a disturbance of flow downstream. Strong cyclonic and anticyclonic meanders in the current about 150 km to the east of the archepelago are evident from a plot of geopotentials at 1000 m depth over the large-grid occupied during April/May 1989 (figure 7).

Perissinotto and Duncombe Rae (1990) estimated that both the initial and frictional terms, as given by the Rossby number (6.6×10^{-2}) and Ekman number (2.6×10^{-5}) respectively, in the equation of motion describing the passage of the ACC past the archipelago are sufficiently small to imply that the flow regime is dominated by geostrophic effects. It was further argued that a Taylor column (a closed streamline anticyclonic vortex that is trapped above a bump under certain conditions of current speed, stratification and topography), could exist as the criteria as set out by Huppert (1975) for current speed and minimum bump height are realised at the Prince Edward archipelago. From further dimensional analysis these authors suggested that the most likely nature of the Taylor column will be such that an anticyclonic eddy is trapped above the plateau, while a cyclonic eddy is shed downstream.

Huppert and Bryan (1976) describe the first effect of an isolated bump on the flow of a non-viscid, stratified fluid. Refering to figure 8, the column of fluid at A is advected to A'. The relatively heavy fluid at the base of A is advected to the top of the topographic feature, which gives rise to a cold (or high density) anomaly trapped above the feature. The doming of the isopycnals at the feature is the uplifting of the dense bottom water toward the surface as the flow follows the bathymetry. This doming causes the high density anomaly and is evident from vertical density profiles at the Prince Edward archipelago (figure 9 - from

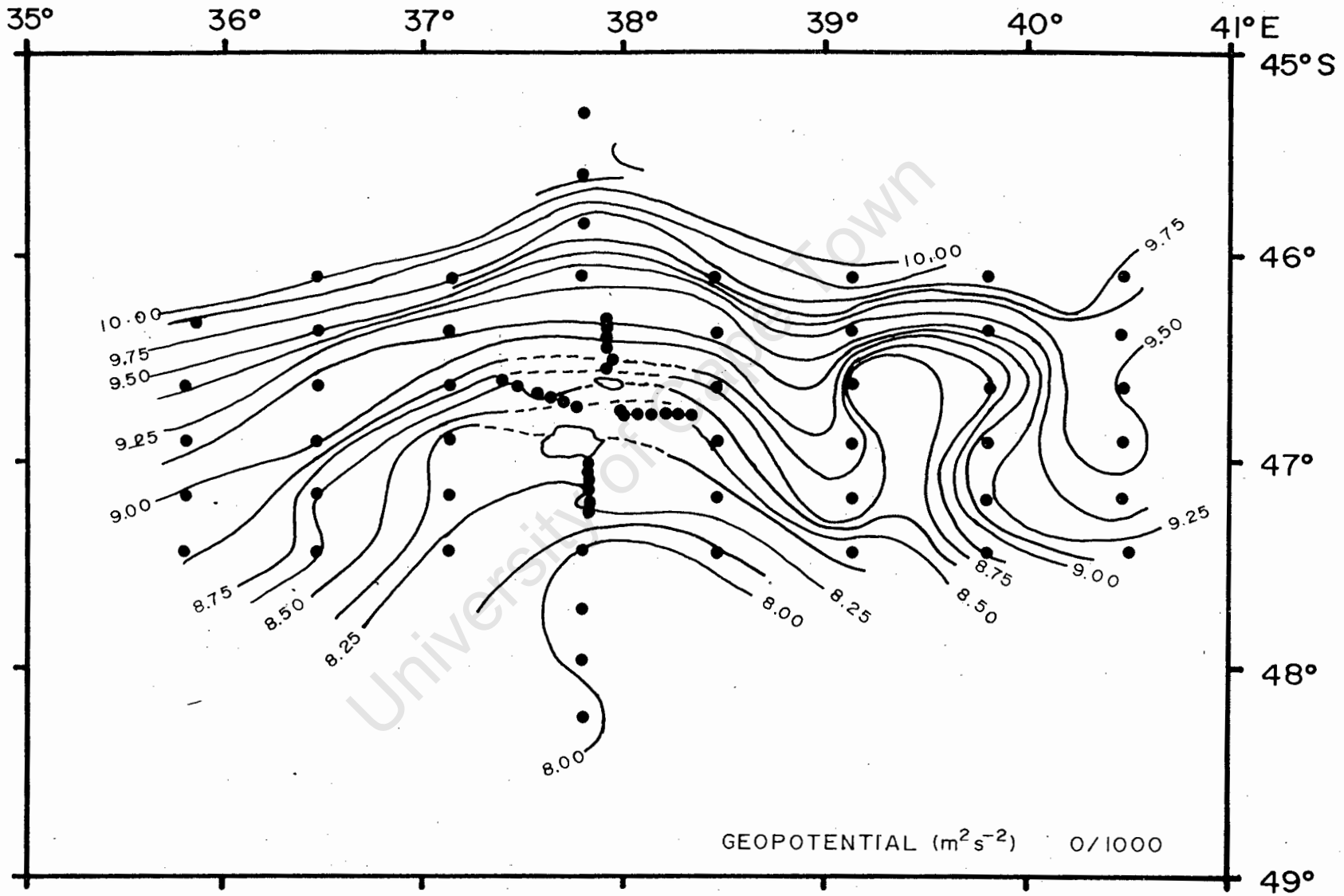

Figure 7: Contoured surface values of geopotentials around the Prince Edward Islands in April/May 1989.

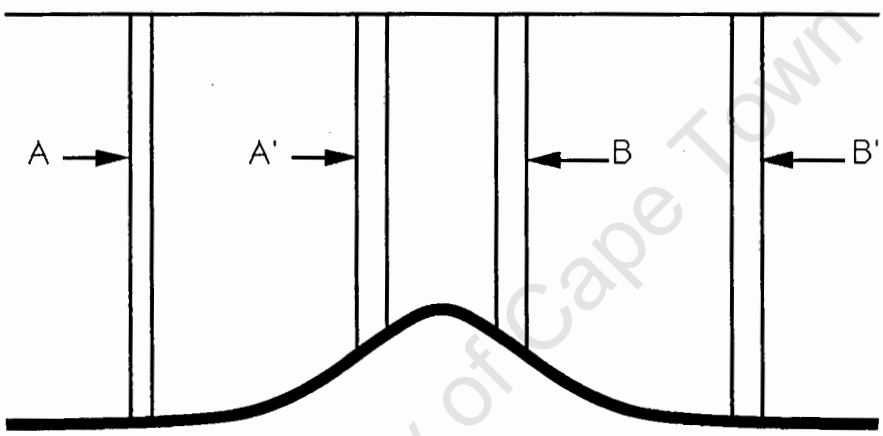

Figure 8. A graphical representation of the effect of an isolated bump on an ocean current. The current flows from left to right. See text for explanation (taken from Huppert & Bryan 1976).

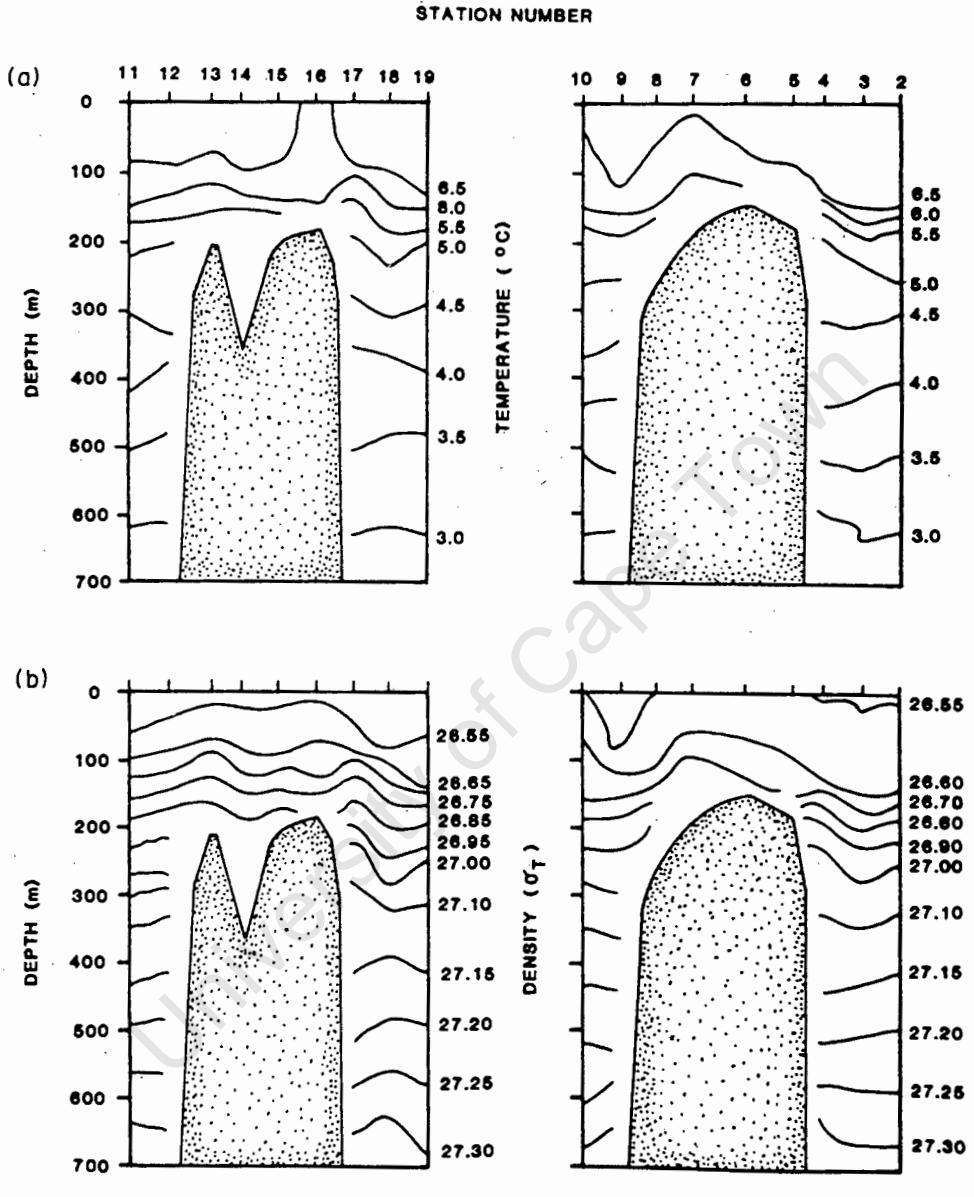

Figure 9: Temperature and density structure along the two east-west CTD transects shown in figure 1 occuppied during April/May 1987 (copied from Perissinotto & Duncombe Rae 1990).

Perissinotto and Duncombe Rae 1990, also Duncombe Rae 1989). Likewise, relatively lighter fluid at B (refering back to figure 8), initially above the feature, sinks as it advects downstream to B' to create a warm (or low density) anomaly. Under conditions of sufficiently strong flow the low density eddy which is shed drifts downstream, otherwise both the cyclonic and anticyclonic eddies remain above the feature. On the basis of their estimate of the Froude number, Perissinotto and Duncombe Rae (1990), argue that, if a Taylor column does exist, this eddy will be shed downstream in the manner described by Huppert and Bryan. Contrary to the statements of Perissinotto and Duncombe Rae (1990), it is the cold anomaly which is retained. *'The cold anomaly remains trapped over the topographic feature, while the shed warm anomaly drifts off downstream for sufficiently large mean flow velocities'* (Huppert and Bryan 1976, p 675). Genin and Boehlert (1985) demonstrated the presence of a cold-dome, similar to a Taylor column, above Minami-kasuga Seamount (21°36'N; 143°38'E) in the Pacific. This did result in a subsurface chlorophyll maximum by uplifting nutrients to within the oligotrophic, euphotic zone.

McCartney (1976) describes an analytical model of an isolated flat-topped bump in the southern hemisphere in a stratified, moving fluid, analogous to the Antarctic circumpolar current (ACC). His solution (figure 5 in McCartney 1976, and redrawn but inverted for the southern hemisphere in figure 7 in Perissonotto et al. 1990) is contrary to that of Huppert and Bryan (1976). An anticyclonic, low density closed streamline develops on the equatorward upstream quadrant above the feature. Above a certain bump-height a closed cyclonic, high density streamline is pinched off downstream on the poleward side of the feature. This prediction is consistent with the theory of Perissinotto and Duncombe Rae (1990).

To apply these models to the Prince Edward archipelago, it is necessary first to compare the physical properties of the system being modelled to that of the archipelago. McCartney's model had the following characteristics:

U_r = 5 cm s^{-1},

f_0 = 10^{-5} s^{-1},

ε < 5×10^{-3},

$$\varepsilon = U_r / (f_0 L), \quad (4)$$

where U_r is the root-mean-square of the current velocity through the water column, L is the horizontal length scale, f_0 is the coriolis parameter and ε is a dimensionless parameter. McCartney's model deals with large L, specifically L > 100 km. From the values used by McCartney in his solution described above, L can be solved for as follows:

$$L\, 5 \times 10^{-3} > U_r / f_0, \quad (5)$$

$$L > 5 \times 10^5 \times 10^3 / 5, \quad (6)$$

$$L > 10^8 \text{ cm, or } 10^3 \text{ km.} \quad (7)$$

As the Prince Edward archipelago measures only about 50 km in the east-west direction, Taylor column theory should be applied very cautiously, and the predictions of McCartney's model cannot be expected to hold at this mesoscale level.

An equally pertinent objection to applying these models to the Prince Edward Islands, one which Duncombe Rae (1989) points out, is that the model describes the effect of a sea-mount, where the height of the sea mount (h_0') relative to the maximum water depth (H),

$$h_0 = h_0'/H \quad (8)$$

is small, viz.

$$h_0 = O(\varepsilon) \sim 0.01 \text{ (McCartney 1976).} \quad (9)$$

For the Prince Edward archipelago

$$h_0 = O(1). \quad (10)$$

Huppert and Bryan (1976) were dealing with a topographic feature between 75 and 800 m in vertical extent, where the maximum water column was 4000 m deep, viz. $h_0 \sim 0.2$. The behaviour of the ACC at the Prince Edward archipelago can adequately be described by an extention of either of these models for $h_0 = O(1)$, though no such work could be found. Some theoretical work has treated the effect of a circular cylinder in a flow in a rotating system, representing an island (eg. Hogg 1972, Gordon and Hughes 1981). Typically, an eddy and doming of isopycnals develop in a wake downstream. In oligotrophic waters this leads to the development of a chlorophyll maximum - eg. Doty and Oguri (1956) documented enrichment around Oahu, Gilmartin and Revelante (1974) noted the same at the Hawaiian Islands and reviewed several other cases, Heywood et al. (1990), using an

acoustic doppler current profiler (ADCP), matched predicted and observed flows for two tropical Indian Ocean islands, one of which supported a chlorophyll maximum in an eddy. In cold nutrient-rich waters, however, isopycnal doming does not enhance phytoplankton growth if nutrients are already in non-limiting concentrations.

If low salinity water is indeed trapped over the Prince Edward Island plateau, it is unlikely to be a consequence of a Taylor column mechanism. Duncombe Rae (1989) and Perissinotto and Duncombe Rae (1990) point out that the density minima (evident on three but possibly five occasions) are evident as depressions in the centre of the domed isopycnals and isotherms in figure's 9 and 10 respectively (from Perissinotto and Duncombe Rae 1990). In the first transect in figure 9 the depression is most clearly seen in the density structure, and follows the bathymetry. No depression is visible from the second transect in figure 9, nor is there a depression in the bathymetry. The four N-S transects in figure 10, seen from the eastern side facing the current, each have a dip in the isotherms which could be explained by the uplifting of isotherms on the edges of the transects as water flows from > 1000 m depth over the 200 m isobath around each island (figure 1). These depressions of isopycnals and isotherms are less likely to be the centre of an anticyclonic low density eddy in the centre of domed isopycnals.

The topographical complexity of the archipelago, and of this region of the southern Indian Ocean as a whole (Deacon 1983), might create eddies of turbulent origin (eg. Lutjeharms and Baker 1980) which could be trapped above the island plateau. However, until such time as either consistent evidence for an eddy is forthcoming, or a sound theoretical argument that predicts such a phenomenon can be formulated, it would be better to regard the island-trapped eddy as a possibility rather than as a working-hypothesis which is used to explain biological phenomena. I might for instance adopt Boden's (1988) more relaxed viewpoint: '*The indications seem to be that the circulation is largely wind-driven and consists of a field of sporadic eddies or a backwater of random vorticity that entrains island run-off nutrients and plankton...*'. But, as there is no correlation between surface salinity and stability integrated over 50, 75 nor 100 m for either the April/May 1987 or April/May 1989 data, the 'island-mass effect' is unlikely to be an eddy entrapping low density water.

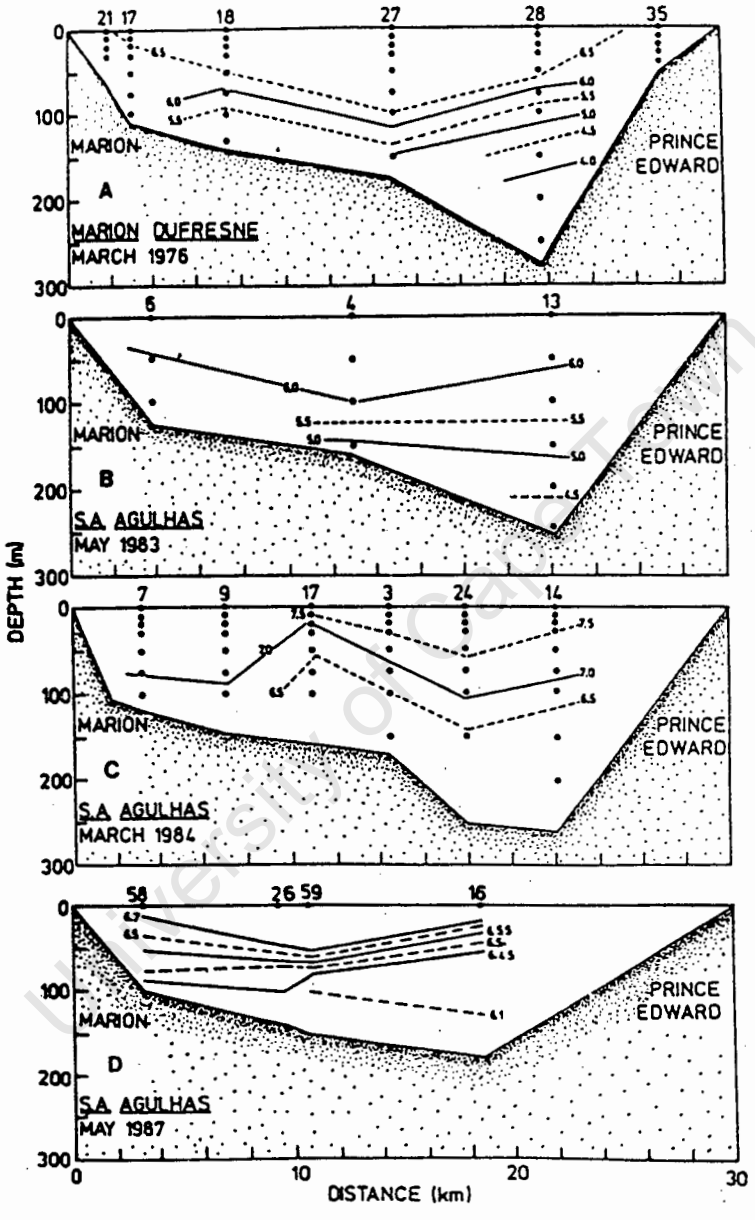

Figure 10: Vertical isotherms (°C) along the north-south transects indicated in figure 1 (taken from Perissinnotto & Duncombe Rae 1990, though transect a, b, c were originally from Parker 1984).

The role of seeding

The species principally responsible for the blooms at the Prince Edward Islands is the diatom *Chaetoceros radicans*, though the diatom *Rhizosolena curvata*, and the silicoflagellate *Dichtyocha speculum* each have been recorded here once in bloom stage. The dominant species (> 10% of total cells) found by El-Sayed et al. (1979a) at Kerguelen Island were the diatoms *Chaetoceros cancavicornis* and *Thalassionema nitzschiodes*, while at the Crozet Islands *Nitschia* spp. were collectively dominant (45% of total cells).

The genus *Chaetoceros*, the richest and most variable genus of truly planktonic diatoms, often is divided into two subgenera, viz. *Phaeoceros* and *Hyalochaete*, the former being oceanic and the latter neritic (Boden and Reid 1989). Only *Haylochaete* species, which include *C. radicans*, commonly form resting spores. This statement must be accepted with some caution, however, as the distinction between oceanic and neritic species is not well defined. Furthermore, the presence of resting spores has long been assumed to characterize a species as neritic (Hargraves and French 1983). The resting spore of *C. radicans* from the Prince Edward Islands is heavily silicified (Fryxell et al. 1981). Boden and Reid (1989) comment that the formation of resting spores is probably the reason why this species blooms so easily. The genus *Rhizosolenia* is known to form resting spores, though it is not known specifically whether *R. curvata* does so. Many of the *Nitschia* diatoms have been noted to be littoral (Boden and Reid 1989).

The two valves of the resting spore are each formed by a mitotic division. *Chaetoceros didymum* accomplishes the formation of both valves by two 'acytokinetic mitoses' (von Stosch et al. 1973, taken from Hargraves and French 1983), i.e. daughter nuclei are seperated but the cell remains undivided. When the spore of this species regerminates, two vegetative cells are produced. The volume of *C. lauderi* was estimated to increase approximately 7-fold during spore-formation (Smayda and Boleyn 1966b). Because of a concomitant reduction in the area/volume ratio, the resting spores of *Chaetoceros lauderi* and of *Rhizosolenia setigera* have been observed to sink faster than their vegetative phases (Smayda and Boleyn 1966a,b). It is believed that the selective advantage of spore formation represents a means by which the cell is able to reach the sea-bed or

thermocline rapidly, where it might survive unfavourable periods and from where it is available for resuspension into surface waters (Smetacek 1985). The formation of spores is known to be triggered by nitrogen deficiency in almost all cases (Hargraves and French 1983). Doucette and Fryxell (1983) have implicated low-light stress as the causal factor in resting spore formation in Antarctic water where nutrient-stress is not believed to occur, though it must be added that this mode of spore formation has yet to be demonstrated in the laboratory for any diatom species.

Bodungen et al. (1986) investigated the fate of diatom blooms in the Bransfield Strait region, Antarctica, particularly with repect to biomass. Four possible reasons for the sudden disappearence of Antarctic phytoplankton stocks were considered: (1) dispersal by mixing and advection, (2) zooplankton grazing, (3) natural mortality/senescence and (4) sinking out of the surface layers. Of these the last explanation seemed most reasonable on account of the occurrence of large numbers of spores in sediment traps deployed at the time. Mixing processes could not have dispersed the bloom to the observed extent and zooplankton populations were patchy and peaked too late in the season for grazing to be a likely explanation. The role of cell senescence was poorly understood and deemed not to be important. Bodungen et al. (1986) argued, as did Smetacek (1985), that the disappearence of the bloom is not to be equated with mortality, but rather with the onset of a dormant resting phase. This hypothesis sheds light on some intriguing influences of bottom topography on surface chlorophyll distributions which cannot be explained by nutrient upwelling (eg. Hayes et al. 1984). Plancke (1977) noted that increases in biomass and productivity, encountered in the vicinity of the Crozet Islands, correspond, to a first approximation, to the extent of the submarine plateau. At Kerguelen he found high biomass and productivity above the 200 m shelf in the northeast, north, and southeast regions and up to the 1000 m contour on the eastern side, but never to the west.

I suggest that the repeated position of a chlorophyll maximum over the Prince Edward and other sub-Antarctic island-shelves can be ascribed to the proximity of the sea bed to the surface waters, and the consequent rapidity with which diatoms can be reseeded into the euphotic zone. The comparative paucity of chlorophyll in the adjacent open ocean may not

be a result of the oceanographic regime being less favourable there than over the island-shelf. Rather, there is not a source for recolonization by diatoms in the open ocean to take advantage of favourable conditions when they do occur as the sediments lie too deep.

This hypothesis is difficult to test at present, and the argument may initially seem somewhat tautological, i.e. blooms of diatoms occur at the Prince Edward Islands because there are many diatoms present. This difficulty could be dismissed by three arguments:

(1) Although the origin of the seeding stock may never be ascertained by direct observational techniques, the flux of resting spores to the sediments can be measured and the occurrence of spores on the sediments can be verified. Unfortunately, the few sediment traps which were deployed during the 1989 cruise of the 'M.V. S.A. Agulhas' to measure downward carbon flux were not successfully recovered, and did not coincide with high chlorophyll concentrations. Results from elsewhere, however, provide proof of a sediment seeding system. Pitcher (1986) showed the vertical profile of resting spore and vegetative cell abundances of six *Chaetoceros* species for the southern Benguela shelf region. The surface layers contained entirely vegetative cells, whereas at the sediment-water interface only resting spores occurred, but with the same proportion of each species. Downward flux of phytoplankton was predominantly in the form of resting spores. Similarly, at one station in the Bransfield Strait Bodungen et al. (1986) found a large number of resting spore frustules of *Thalassiosira* spp. and also sand grains in their sediment traps at 50 and 100 m from the bottom, providing evidence for a turbulent process which can resuspend dormant resting spores.

(2) The diatom species which bloom at the Prince Edward Islands have a potent mechanism for sinking to the sediment. In this way they are able to maintain an endemic population. The repeated occurrence of *C. radicans* over the Prince Edward Island plateau is suggestive of this; each time phytoplankters were identified (March 1976, May 1983, November 1983, April/May 1987) *C. radicans* was found to dominate the bloom.

A similar recurrence of a diatom bloom has been recorded in the waters overlying the edge of the continental shelf in Prydz Bay, Antarctica. In this region the diatom *Thalassiothrix longissima* formed a subsurface bloom on three separate occasions (8 and 14

February 1982 and 2 March 1983) within 00°06' latitude and 01°26' longitude of each other (Quilty et al. 1985). On each occassion the bloom registered on the ship's echo-sounder; on the first encounter it measured 4.6 nautical miles long. What is of even more interest is that Admiralty Chart 3171, compiled prior to 1974, recorded a shoaling in the topography at this exact locality (where none exists), marked 'existence doubtful'. Apparently this subsurface bloom had been mistakenly recorded many years before.

(3) From numerical arguments it is easy to demonstrate that at a finite time after an episodic event (eg. deep mixing or upwelling) the strength of net-plankton populations is sensitive to its starting biomass. Moloney and Field (1991) describe the results of a size-structured simulation model, and discuss the importance of initial values of net-plankton for subsequent outcomes. As Bodungen et al. (1986) rightly pointed out, the magnitude of a given phytoplankton bloom is a function of the specific growth rate and the initial seed population. An interesting extention of this idea would be to model primary production, taking into consideration phytoplankton recruitment into surface waters as a determinant of carbon fixation.

The existence of an endemic phytoplankton population (i.e. one with some degree of genetic integrity) at the Prince Edward Islands might seem unlikely. An equivalent problem confronts biologists with respect to the high degree of endemism among the benthic community on the shallow sea-bed at the Prince Edward Islands. The enigma is that many of the endemic species are broadcast spawners with pelagic larvae (G.M. Branch, Zoology Department, University of Cape Town, personal communication). In this sense these endemic benthic invertebrates are similar to the spore-forming diatoms, both maintaining localised populations in spite of having pelagic life stages. Planktonic forms at the Prince Edward Islands apparently are not swept away as rapidly as one would expect if there were no retention mechanism. However, until the results of a drogue-study in this region can consider , it is impossible to be dogmatic. I contend that the Prince Edward 'island-mass effect' is simply due to the resuspension of dormant diatom spores and that it is unnecessary to invoke complex oceanographic processes.

References

Allanson B.R., B. Boden, L. Parker and C. Duncombe Rae (1985) A contribution to the oceanology of the Prince Edward Islands. In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried, P.R. Condy and R.M. Laws, editors, Springer-Verlag, Berlin, pp. 38-45.

Allanson, B.R., R.C, Hart and J.R.E. Lutjeharms (1981) Observations on the nutrients, chlorophyll and primary production of the Southern Ocean south of South Africa. *S. Afr. J. Antarct. Res.*, 10/11, 3-14.

Beardall, J. and I. Morris (1976) The concept of light intensity adaptation in marine phytoplankton: some experiments with *Phaeodactylum tricornutum*. *Mar. Biol.*, 37, 377-387.

Boden, B.P. (1988) Observations of the Island mass effect in the Prince Edward Archipelago. *Polar Biol.* 9, 61-68.

Boden, B.P. and L.D. Parker (1986) The plankton of the Prince Edward Islands. *Polar biol.*, 5, 81-93.

Boden, B.P.and F.M.H. Reid (1989) Marine plankton diatoms between Cape Town and the Prince Edward Islands (SW Indian Ocean). *S. Afr. J. Antarct. Res.*, 19(2), 2-49.

Bodungen, B.v., V.S. Smetacek, M.M. Tilzer and B. Zeitzschel (1986) Primary production and sedimentation during spring in the Antarctic Peninsula region. *Deep-Sea Res.*, 33(2), 177-194.

Deacon, G.E.R. (1983) Kerguelen, Antarctic and subAntarctic. *Deep-Sea Res.*, 30(1), 77-81.

Doucette, G.J.and G.A. Fryxell (1983) *Thalassiosira antarctica*: vegetative and resting stage composition of an ice-related marine diatom. *Mar. Biol.*, 78, 1-6.

Doty, M.S. and M. Oguri (1956) The island mass effect. *Journal du Conseil. Conseil Permanent International pour l' Exploration de la Mer*, 22, 33-37.

Duncombe Rae, C.M. (1989a) Physical and chemical marine environment of the Prince Edward Islands (southern ocean) during April/May 1987. *S. Afr. J. Mar. Sci.*, 8, 301-311.

Duncombe Rae, C.M. (1989b) Data report of the first cruise of the Marion Off-shore Ecological Study (MOES-I). *South African National Scientific Progress Report*, 159, pp. 384.

El-Sayed, S.Z. and H.R. Jitts (1973) Phytoplankton production in the southeastern Indian Ocean. In: *Ecological studies*, B. Zeitzschel, editor, Springer-Verlag, 11, 131-142.

El-Sayed, S.Z., D.A. Stockwell, H.A. Reheim, S. Taguchi and M.A. Meyer (1979a) On the productivity of the Southwestern Indian Ocean. *C. N. F. R. A.*, 44, 83-110.

El-Sayed, S.Z., P. Benon, P. David, J.R. Gridley and J-F. Murial (1979b) Some aspects of the biology of the water column studied during the 'Marion Dufresne' cruise 08. *C. N. F. R. A.*, 44, 127-134.

Fryxell, G.A., T.A. Villareal and G.J. Doucette (1981) Diatom resting spores and Agulhas collections. *Antarct.J. U. S.*, 16, 128-130.

Fukuchi, M. (1977) Chlorophyll-*a* content in the surface water along the course of the Fuji to and from Antarctica in 1976-1977. *Polar Rec.*, 60, 57-69.

Fukuchi, M.and S. Tamura (1982). Chlorophyll-*a* distribution in the Indian sector of the Antarctic Ocean in 1978-1979. *Polar Rec.*, 74, 143-162.

Gilmartin, M. and N. Revelante (1974) The island mass effect on the phytoplankton and primary production of the Hawaiian islands. *Journal of Experimental Mar. Biol. and Ecology*, 16, 181-204.

Gordon, H.B. and R.L. Hughes (1981) A study of rotating baroclinic nonlinear flow around an island. *Journal of Physical Oceanography*, 11, 1011-1014.

Grindley, J.R. (1978) Marine ecosystems of Marion Island. *South African Journal of Antarctic Research*, 8, 38-42.

Grindley, J.R. and P. David (1985) Nutrient upwelling and its effect in the lee of Marion Island. In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried, P.R. Condy and R.M. Laws, editors, Springer-Verlag, Berlin, pp.46-51.

Grindley, J.R. and S.B. Lane (1979) Zooplankton around Marion and Prince Edward Islands. *C. N. F. R. A.*, 44, 111-125.

Hargraves, P.E. and F.W. French (1983) Diatom resting spores: significance and strategies. In: *Survival strategies of the algae*, G. A. Fryxell, editor, Cambridge University Press, pp. 49-68.

Harris, G.P. (1986) *Phytoplankton ecology. Structure, function and fluctuation.* Chapman and Hall, London, 360 pp.

Hayes, P.K., T.M. Whitaker and G.E. Fogg (1984) The distribution and nutrient status of phytoplankton in the southern ocean between 20° and 70° W. *Polar biol.*, 3, 153-165.

Heywood, K.J., E.D. Barton and J.H. Simpson (1990) The effects of flow disturbance by an oceanic island. *J. Mar. Res.*, 48(1), 55 - 73.

Hogg, N.G. (1972) Steady flow passed an island with application to Bermuda. *Geophysical Fluid Dynamics*, 4, 55-81.

Holm-Hansen, O. (1985) Nutrient cycles in Antarctic ecosystems. In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried, P.R. Condy and R.M. Laws, editors, Springer-Verlag, Berlin, pp. 6-10.

Hoshino, T. (1974) Surface water Chlorophyll-*a* contents observed during the cruise of the Fuji to Antarctica, November 1973-April 1974. *Polar Rec.*, 51, 29-38.

Huppert, H.E. (1975). Some remarks on the initiation of inertial Taylor columns. *J. of Fluid Mech.*, 67, 397-412.

Huppert, H.E. and K. Bryan (1976) Topographically generated eddies. *Deep-Sea Res.*, 23, 665-679.

Jacques, G., G. De Billy and M. Panouse (1982) Biomasse et production primaire dans les secteurs antarctique et subantarctique de l'ocean Indien (Mars 1980). *C. N. F. R. A.*, 53, 87 - 99.

Kuroda, K. (1978) Distribution of chlorophyll-*a* contents in the surface water along the course of the Fuji to and from Antarctica in 1972-1973. *Polar Rec.*, 61, 65-74.

Lutjeharms, J.R.E. and D.J. Baker Jr. (1980) A statistical analysis of the meso-scale dynamics of the Southern Ocean. *Deep-Sea Res.* 27, 145-159.

Lutjeharms, J.R.E. and H.R. Valentine (1984) Southern Ocean thermal fronts south of Africa. *Deep-Sea Res.*, 31(12), 1461-1475.

Lutjeharms, J.R.E., N.M. Walters, and B.R. Allanson (1985) Oceanic frontal systems and biological enhancement. In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried, P.R. Condy and R.M. Laws, editors, Springer-Verlag, Berlin, pp. 11-21.

McCartney, M.S. (1976) The interaction of zonal currents with topography with applications to the southern ocean. *Deep-Sea Res.*, 23, 413-427.

Millard, R.C., W.B. Owens and N.P. Fofonoff (1990) On the calculation of the Brunt-Vaisala frequency. *Deep-Sea Res.*, 37(1), 167-181.

Miller, D.G.M., B.P. Boden and L. Parker (1984) Hydrology and bio-oceanography of the Prince edward Islands (south west Indian Ocean). *S. Afr. J. Antarct. Res.*, 14, 29-31.

Moloney, C.L. and F.G. Field (1991) The size-based dynamics of plankton food webs. I. A simulation model of carbon and nitrogen flows. *J. Plankt. Res.*, in press.

Nishiwaki, S. (1972) Chlorophyll-*a* content in the sea surface water observed in 1970-1971 during the cruise of Fuji to Antarctica. *Polar Rec.*, 44, 93-99.

Ohno, M. (1976) Chlorophyll-*a* content in the surface water observed during the cruise of the Fuji to Antarctica in 1974-1975. *Polar Rec.*, 57, 106-114.

Ohyama, Y. and T. Mayama (1976) Chlorophyll-*a* contents in the surface water observed during the relief voyage of Fuji to Syowa Station, Antarctica, in 1975-1976. *Polar Rec.*, 57, 115-122.

Olson, R.J. (1980) Nitrate and ammonium uptake in Antarctic water. *Limnol. Oceanogr.*, 25, 1064-1074.

Parker, L.D. (1984) A contribution to the oceanology of the Prince Edward Islands. unpublished M.Sc. Thesis, Rhodes University, Grahamstown, South Africa, 84 pp.

Perissinotto, R. and B.P. Boden (1989) Zooplankton-phytoplankton relationships at the Prince Edward Islands during April/May 1985 and 1986. *S. Afr. J. Antarct. Res.*, 19(1), 26-30.

Perissinotto, R. and C.M. Duncombe Rae (1990) Occurrence of anticyclonic eddies on the Prince Edward Plateau (South Ocean): effects on phytoplankton biomass and production. *Deep-Sea Res.*, 37(5), 777-793.

Perissinotto, R., C.M. Duncombe Rae, B.P. Boden and B.R. Allanson (1990) Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago. *Mar. Ecol. Prog. Ser.*, 60, 205-209.

Pitcher, G.C. (1986) Sedimentary flux and the formation of resting spores of selected *Chaetoceros* species at two sites in the southern Benguela System. *S. Afr. J. Mar. Sci.*, 4, 231-244.

Plancke, J. (1977) Phytoplankton biomass and productivity in the subtropical convergence area and shelves of the Western Indian sub-Antarctic Islands. In: *Adaptations within Antarctic ecosystems: Proceedings of the third SCAR Symposium on Antarctic Biology*, G.A. Llano, editor, pp. 51-73.

Platt, T. and A.D. Jassby (1976) The relationship between photosynthesis and light for natural coastal marine phytoplankton. *J. Phycol.*, 12, 421-430.

Prezelin, B.B. (1981) Light reactions in photosynthesis, p. 1 - 43. In: Physiological bases of phytoplankton ecology. *Can. Bull. Fish. Aquat. Sci.*, 210, 1-43.

Priddle, J., R.B. Heywood and E. Theriot (1986) Some environmental factors influencing phytoplankton in the southern ocean around South Georgia. *Polar biol.*, 5, 65-79.

Probyn, T. and S.J. Painting (1985) Nitrogen uptake by size-fractionated phytoplankton populations in Antarctic surface waters. *Limnol. Oceanogr.*, 30, 1327-1332.

Quilty, P.G., K.R. Kerry and H.J. Marchant (1985) A seasonally recurrent patch of Antarctic planktonic diatoms. *A.N.Z.A.A.S.*, 16(1-2), 48.

Smayda, J.T. and B.J. Boleyn (1966a) Experimental observations on the floatation of marine diatoms. II *Skeletonema costatum* and *Rhizosolenia setigera*. *Limnol. Oceanogr.*, 11, 18-34.

Smayda, J.T. and B.J. Boleyn (1966b) Experimental observations on the floatation of marine diatoms. II *Bacteriastrum hyalinum* and *Chaetoceros lauderi*. *Limnol. Oceanogr.*, 11, 35-43.

Smetacek, V. (1985) Role of sinking in diatom life-history cycles: ecological, evolutionary and geological significance. *Mar. Biol.*, 84, 239-251.

Steenman-Nilsen, E. (1952) The use of radioactive carbon (^{14}C) for measuring organic production in the sea. *Journal du Conseil. Conseil Permanent International pour l' Exploration de la Mer*, 18, 117-140.

Strickland, J.H.D. and T.R. Parsons (1972) A practical handbook of seawater analysis. *Bull. Fish. Res. Bd. Can.*, 167, 1-113.

Tanimura, A. (1981) Distribution of the surface chlorophyll-*a* along the course of the Fuji to and from Antarctica in 1979-1980. *Polar Rec.*, 72, 35-42.

Tominaga, H. (1971) Chlorophyll-*a* and phaeophytin contents in the surface water of the Antarctic ocean through the Indian Ocean. *Polar Rec.*, 42, 124-134.

Treguer, P. (1985) Comparative physical and chemical characteristics of coastal waters from Kerguelen and Heard Islands and their oceanic surroundings during summer relation to phytoplankton growth. *C. N. F. R. A.*, 57, 17-26.

Van Ballegooyen, R., R. Perissinotto, H. Ismael, B. Boden, B. Allanson, M. Lucas and J.R.E. Lutjeharms (1989) *Data report of the second cruise of the Marion Off-shore Ecological Study (MOESS-II).* CSIR Report EMA-D 8910, EMATEK, PO Box 320, Stellenbosch, South Africa.

von Stosch, H.A., G. Theil, and K. Kowallik (1973) Entwicklungsgeschichtliche Untersuchungen an zentrischen Diatomeen. V. Bau und Lebenszyclus von *Chaetocers didymum* mit Boebachtunger uber einige andere Arten der Gattung. *Helgolander Wissenschaftliche Meeresuntersuchungen*, 25, 384 - 445.

Watanabe, K. and Y. Nakajima (1983) Surface distribution of Chlorophyll-*a* along the course of the Fuji (1980/81) in the Southern Ocean. *Polar Rec.*, 77, 33-39.

Yamagata, K. and F. Fukui (1981) Chlorophyll-*a* content in the Indian sector of the Antarctic Ocean. *Polar Rec.*, 73, 72-81.

Yentsch, C.S. and R.W. Lee (1966) A study of photosynthetic light reactions and a new interpretation of sun and shade phytoplankton. *J. Mar.Res.*, 24, 319-337.

Chapter 2

Ecological indications of the lipid content and composition of sub-Antarctic euphausiids and copepods

Abstract-The lipid content, class composition and fatty acid composition of 8 euphausiid and 2 large copepod species were investigated from samples of the sub-Antarctic Indian ocean. The lipid contents of the euphausiids were low compared to congeners from higher latitudes, especially considering that the samples were taken in late summer. The copepods were, however, richer in lipids. Surface chlorophyll-*a* in the sub-Antarctic is low when compared to the oceanic fronts to the north and south, suggesting that this region is not a productive feeding environment for zooplankton. Most species in this region occur here at the extreme of their known ranges. *Thysanoessa vicina*, *T. macrura*. and *Metridia* spp. were found to contain wax esters in abundance, whereas *Euphausia* spp. and *Nematoscelis megalops* and *T. gregaria* stored no wax ester. The fatty acid composition points to a herbivorous diet for all specimens examined, though it is likely that those lipid-poor species which do not store wax ester will switch to an alternative winter diet. Furthermore, the sub-tropical *Thysanoessa gregaria* and *Metridia lucens* contained little or less wax ester compared to their congeners of the Antarctic, which presumably reflects the different feeding strategies associated with latitudinal differences. A herbivorous diet of sub-Antarctic euphausiids would imply that the large sea-bird populations of this region, which feed principally on euphausiids, end a very short oceanic food chain, though the role of microzooplankton in this food chain remains unknown.

Introduction

Variation in the quantity and composition of neutral (storage) lipids within copepod and euphausiid species can be explained in terms of their life cycle (eg. Kattner and Krause 1987), breeding condition (eg Clarke 1980), and integrated feeding history (eg. Ohman 1988; Willason et al. 1986). Variation in the neutral lipid composition between species, and in some cases between populations which are geographically separated, concerns most notably the presence or absence of wax ester. It has been hypothesised (Lee et al. 1971) that the synthesis of wax ester as a long-term storage medium can be coupled to a particular life history strategy of herbivorous zooplankton in strongly seasonal (i.e. polar) environments. The explanation advanced by Sargent and McIntosch (1974) for this long-term storage medium being wax ester, rather than the conventional triacylglycerol, involves the rate-limiting step in the biosynthesis of fatty acids from monosaccharides of photosynthetic origin. During periods of food availability, the rapid and prolonged synthesis of fatty acids is inhibited by an accumulation of the reducing agents, NADH and NADPH. This end-product inhibition can be removed by the simultaneous conversion of fatty acid into fatty alcohol which reduces NADH and NADPH. The so formed fatty alcohols esterify with fatty acids to form wax esters. The synthesis of triacylglycerol (which includes no fatty alcohol) cannot proceed at a rate fast enough to create a large lipid storage required for overwintering from short periods of high food concentration. Planktonic herbivores which do not store wax esters are presumably switching to alternative winter food sources (zooplankton or detritus) or do not experience a short supply of phytoplankton in winter.

Certainly all copepod species seem to synthesise wax esters. Sargent and Henderson (1986) list 27 species from ten genera, of which all contained wax esters. They did however point out the trend that polar copepods contain a greater proportion of their lipids as wax esters than those of temperate and subtropical waters. In the genus *Calanus* for instance wax esters reach up to 92% of total lipid. The hypothesis of Lee et al. (1971) seems to hold for euphausiids also. *Thysanoessa inermis* of the Arctic is richer in wax ester than its congener *T. raschii* of more southerly distribution. In the Antarctic *Euphausia crystallorophias*, whose distribution extends to the ice-edge, is rich in wax ester, but of the sympatric *E.*

superba it can be said that this species entirely lacks wax esters (Clarke 1980). *E. superba* apparently is omnivorous (Price et al. 1988). The carnivorous *Meganctyphanes norvegica* also lacks wax ester (Sargent and Falk-Peterson 1981).

The fatty acids of phytoplankton are present predominantly in glycolipids, the major constituent of the thylakoid membrane of chloroplasts (Harwood and Russell 1984). Fatty acids of Arctic phytoplankton communities, including a mixture of *Phaeocystis pouchetii* and diatoms (*Chaetoceros* spp. and *Nitzschia grunowi*), were found to contain 14:0 and 16:0 chains (together about 30%), monounsaturates (both ω7 and ω9) and a variety of long chain ω3 polyunsaturates which constitute some 40% of the fatty acid composition (Sargent et al. 1985). Schofield et al. (1982) identified a Type I fatty acid synthetase (present in all animals thus far studied) in *Calanus finmarchicus*, with the major *in vitro* end products being 16:0, 18:0 and 20:0. The presence in calanoids of a Δ^9 desaturase enzyme implies that monounsaturates, in particular 18:1(ω9), 20:1(ω9) and 22:1(ω11), can also be biosynthesised, the latter two being chain lengthened in addition (Sargent and Henderson 1986). These authors then discussed the evidence, in particular the high occurrence of ω3 polyunsaturates, to suggest that the fatty acids of wax ester of *C. finmarchicus* were, nonetheless, predominantly of phytoplanktonic origin. The phospholipid fatty acids of calanoids are also rich in ω3 polyunsaturates.

The fatty alcohols of wax esters of *Calanus* tend to be predominantly long chain saturates and monounsaturates, notably C_{18}, C_{20} and C_{22} chains (Lee 1974, 1975, Prahl et al. 1984). These are converted from the equivalent fatty acids, which are synthesised *de novo*. The alcohols are then esterified with short chain saturated and long chain unsaturated fatty acids of phytoplanktonic origin. It has thus been suggested that wax ester formation is a means for allowing lipogenesis to proceed in a continuing input of dietery lipid (Sargent and Henderson 1986).

Whereas the fatty acid and alcohol composition described above applies to herbivorous calanoids, carnivorous zooplankton are noticably different (i.e. krill, Sargent and Falk-Peterson 1981; copepods, Falk Peterson et al. 1987). Here the dominant neutral lipid is triacylglycerol, the fatty acids of which are rich in long chain monounsaturates, 18:1, 20:1

and 22:1. These would have been converted from the fatty alcohols of their herbivorous prey, for as fatty acids, these precursors are absent in phytoplankton and are only an intermediate step in the synthesis of fatty alcohols in herbivores.

Other indicators of trophic position include the monounsaturates, 16:1(ω7) and 18:1(ω7). Both these molecules must have their origin as 16:0 found in phytoplankton if the desaturase enzyme operates with a Δ^9 specificity (Sargent and Falk-Peterson 1981). Their strong presence would indicate a phytoplanktonic rather than an animal dietary origin. Falk-Peterson et al. (1981) showed that for *Metridia longa*, an omnivorous copepod, the levels of 16:1(ω7) fatty acids decreased through winter, coinciding with a lower phytoplanktonic fraction in the diet. The carnivorous euphausiid, *Meganyctiphanes norvegica*, on the other hand, has more of 18:1(ω9) formed by the desaturation of 18:0 of animal orgin, than the sympatric herbivorous euphausiids *Thysanoessa inermis* and *T. raschii* (Sargent and Falk-Peterson 1981). The ratio of these isomers of 18:1 is believed to be an indication of the diet.

Although we cannot take these trends to be general principles, the lipid composition might tell us something about zooplankton life history strategies and trophic dynamics which are otherwise difficult to resolve. This paper presents the results of lipid analyses, including estimation of lipid fractions by densitometry and gas chromatography of the constituent fatty acids, performed on specimens of eight species of euphausiids, *Euphausia vallentini* Stebbing, *E. similis* v. *armata* Hansen, *E. hemigiba* Hansen, *E. longirostris* Hansen, *Nematoscelis megalops* G.O. Sars, *Thysanoessa vicina* Hansen, *T. gregaria* G.O. Sars and *T. macrura* G.O. Sars, and two copepod species, *Metridia gerlachei* Giesbrecht and *M. lucens* Boeck, caught in the vicinity of the Prince Edward Islands in the southern Indian Ocean between the latitudes of 45° and 49°S. The specimens were collected in April/May (late summer-early winter) when it is to be expected that zooplankton are replete with lipids.

Of particular interest was how a large and diverse zooplankton community could exist in sub-Antarctic water, which is nutrient rich but, unlike Antarctic water, is unstable perenially, with low chlorophyll concentration. This zooplankton community supports a vast biomass of oceanic avian predators. The adaptations of these sea-birds' gut enzymes to lipid rich diets have already been investigated (Jackson and Place, in press). It was envisaged that

a detailed analysis of the lipids of the dominant macro-zooplankton might give some further indication of the trophic dynamics of this sub-Antarctic pelagic ecosystem.

Material and Methods

This study is based on material collected on the second Marion Island Off-shore Ecological Study (MOES II) cruise of the M.V. S.A. Agulhas, dated 30/03/1989 to 09/05/1989, between the latitudes of 45°17'S and 48°14'S, and the longitudes of 46°38'E and 40°30'E. Zooplankton was collected with a bongo net with mesh sizes of 300µm and 500µm. The times of collection varied. Day-time oblique hauls were extended to a depth of 300m; night-time hauls were extended to a depth of 100m. Animals were carefully removed and identified in a petri-dish under a light microscope. Once identified the specimens were sealed in plastic vials and frozen at -25°C. Upon return to Cape Town the samples were transfered to a -80°C freezer. The procedures outlined below were completed in the ensuing 12 months.

Prior to analysis, specimens were thawed and wet-weighed collectively for each species. I thus have no measure of variability of mass or lipid content within species. No attempt was made to differentiate the sexes. Total lipid was extracted by the method of Bligh and Dyer (1959) in chloroform-methanol. The final solution contained a 40ml chloroform-lipid layer, 20ml of which was pipetted into a pre-weighed flask and evaporated under vacuum in a water bath at 70°C. The flask with lipid was weighed again and the increase in mass was taken to be half the mass of the total extracted lipid.

Lipid classes were separated by thin layer chromatography (TLC) using pre-coated TLC plates (Silica gel 60/ Kieselguhr F254) and identified from standards. The solvent was a mixture of hexane (85 parts), diethyl ether (15 parts) and acetic acid (1 part). After develoment, the plates were immersed in a charring agent consisting of cupric acetate (3 parts), phosphoric acid (8 parts) and water (89 parts), and heated at 130°C for 15 minutes. The plates were scanned by a densitometer with an oscillating light beam and the output plotted graphically. The relative area under each peak represented the proportion of each lipid class.

Samples of each lipid class were scraped from 2-dimensional TLC plates for gas chromatography. Lipids were eluted into a flask with chloroform, filtered through a Whatman 41 filter to remove the silica and then the chloroform was evaporated. To the lipid residue 5ml 0.5 M NaOH in methanol was added. The solution was heated under reflux for 5 - 10 minutes to saponify the fatty acids. Thereafter, 5ml Boron trifluoride-methanol complex (20% in methanol) was added and the solution was refluxed for a further 5 minutes to prepare methyl esters. Hexane AR (5 ml) was finally added and the solution refluxed for a further 5 minutes and then allowed to cool before filling with saturated aqueous NaCl. The hexane layer was allowed to separate and this was transfered with a Pasteur pipette into a 5ml sample bottle. The solvent was completely evaporated under a stream of nitrogen gas. 0.5 ml Hexane was added. From this final solution 2µl was injected into a 5710A Hewlett Packard gas chromatograph with hydrogen as the carrier gas. The injection port temperature was 250°C, detector temperature 300°C and the temperature gradient 150°C - 280°C at 4°C per minute. The column was a 40m open tubular OV 73 capillary column. Peaks were integrated on a Spectra-Physics SP 4290 Integrator. The analytical precision of this particular instrument is good, the coefficient of variation of replicate samples beng less thn 5% (Wagener et al. 1984)

Results

The wet masses and percentage lipid of each species are listed in table 4. Studies on other species of euphausiids (Sargent and Falk-Peterson 1981, Clarke 1980) have shown no marked differences with respect to these parameters between the sexes, provided females have not recently spawned. Being constrained by small sample sizes for at least five of the species, it was decided not to attempt separating sexes, but rather to pool individuals. The values listed are thus the mean of the sample.

Table 5 lists the total lipid composition as estimated by densitometry. For each plate there were five samples, the central of which was the zooplankton sample, the other four were standards. These standards were respectively cholesterol, free fatty acid, orange roughy (*Hoplostethus atlanticus*) oil rich in wax ester and anchovy (*Engraulis capensis*) oil

rich in triacylglycerol. The origin zone was taken as phospholipids, thereafter occurred mono- and diacylglycerol (the two were indistinguishable), cholesterol, free fatty acid, alcohol (these last two being indistinguishable on the plates), triacylglycerol and finally wax ester.

Little or nothing is known of the timing of the breeding cycle for any of the species examined in this study. The *Euphausia* species of Antarctic water display a strongly seasonal pattern in the development of their ovaries, whereas *E. lucens* and *E. hanseni* of the cool Benguela current, north of the sub-Antarctic, spawn year round (Pillar and Stuart 1988, Barange and Stuart, in prep.). None of the female *Euphausia* spp. nor *Thysanoessa gregaria* specimens examined were obviously gravid. Although the ovaries were visible through the cuticle in the live animals, they did not extend into the first abdominal segment and caused no marked swelling of the thorax. The ovaries of *Nematoscelis megalops* were not clearly visible.

Because the total lipid and fatty acid composition is similar within each of the four genera, the results with respect to each genus will be presented separately.

Euphausia spp.

None of the four species contained wax ester, except for a trace amount in *E. similis* v. *armata*. Triacylglycerol content ranged from 1.1% wet mass in *E. longirostris* to 19.9% in *E. similis* v. *armata*. Free fatty acids were major components (20-40% wet mass). The mono- and diacylglycerol levels were substantial and similar to those of some euphausiids (Sargent and Falk-Peterson 1981), but far greater than that reported for *E. superba* (Clarke 1980). Phospholipids ranged between 25% and 40%, while free sterols were generally less than half this value. Of the four species *E. longirostris* had the lowest triacylglycerol content, but a high partial glyceride content. It also contained the least lipid of the four *Euphausia* species. Although a comparison between species is not strictly valid, there appears to be a positive relationship between percentage lipid and triacylglycerol.

Table 4. Individual wet mass and lipid content (percent of wet mass) of pooled samples of euphausiid and copepod species from the sub-Antarctic.

Species	Wet mass (mg)	% Lipid	n	Date and location of capture
Euphausia vallentini	53.6	2.39	10	10-04-89;46°53'S,37°07'E
			5	15-04-89;45°17'S,37°48'E
			17	24-04-89;46°49'S,38°01'E
			15	02-05-89;46°40'S,37°42'E
E. similis v. armata	41.4	2.81	4	19-04-89;46°05'S,40°28'E
			15	24-04-89;46°49'S,37°55'E
			35	28-04-89;46°38'S,37°37'E
			10	29-04-89;46°53'S,37°07'E
			10	03-05-89;46°40'S,37°42'E
E. hemigibba	44.8	2.04	9	08-04-89;47°26'S,35°48'E
			3	10-04-89;46°22'S,37°07'E
E. longirostris	214.6	1.33	4	17-04-89;46°38'S,39°48'E
			2	28-04-89;46°38'S,37°37'E
Nematoscelis megalops	86.9	1.50	10	08-04-89;46°22'S,35°48'E
			3	16-04-89;47°10'S,38°10'E
			7	09-04-89;46°38'S,40°28'E
Thysanoessa vicina	6.5	3.19	20	16-04-89;46°54'S,39°07'E
			13	17-04-89;46°38'S,39°48'E
T. gregaria	32.7	3.40	4	15-04-89;45°17'S,37°48'E
T. macrura	5.8	2.80	8	11-04-89;48°14'S,37°48'E
			2	10-04-89;46°53'S,37°07'E
Metridia gerlachei	0.76	14.09	15	08-04-89;46°26'S,35°48'E
			15	15-04-89;46°22'S,38°27'E
			20	24-04-89;46°48'S,37°59'E
			25	28-04-89;46°38'S,37°37'E
			15	02-04-89;46°40'S,37°42'E
M. lucens	0.46	6.70	15	09-04-89;47°10'S,36°28'E
			10	10-04-89;46°53'S,37°07'E
			20	24-04-89;46°49'S,37°59'E

Table 5. The lipid composition (expressed as a percentage of total lipid) of euphausiids and copepods from the sub-Antarctic, April/May 1989. PL = phospholipid, FFA = free fatty acids and alcohol, MGandDG = mono- and diacylglycerol, CL = cholesterol, TG = triacylglycerol, WE = wax ester. tr = trace amount undetected by the oscilating densitometer scanner, but faintly visible.

Species	PL	FFA	CL	MG & DG	TG	WE
Euphausia vallentini	25.2	42.0	12.9	1.7	18.2	0.0
E. similis v. armata	12.8	20.1	6.7	3.88	19.9	tr
E. hemigibba	29.7	41.9	21.4	tr	7.0	0.0
E. longirostris	41.9	32.8	14.8	9.4	1.1	0.0
Nematoscelis megalops	59.8	10.8	11.9	17.5	tr	0.0
Thysanoessa vicina	17.7	38.0	10.8	1.5	2.2	29.8
T. gregaria	41.4	34.1	10.1	8.1	6.3	tr
T. macrura	25.9	32.6	22.9	5.4	5.2	8.0
Metridia gerlachei	8.7	11.9	7.3	4.4	18.0	49.7
M. lucens	10.1	tr	13.5	2.7	47.9	25.8

Table 6 lists the fatty acid composition of the phospholipid, free fatty acid and triacylglycerol fractions of *E. vallentini* and *E. similis* v. *armata*. The small sample sizes of *E. hemigibba* and *E. longirostris* did not provide sufficient of each of the lipid classes to analyse the fatty acid composition of these two species. 14:0 and in particular 16:0 fatty acids were well represented in all lipid classes of both *E. vallentini* and *E. similis* v. *armata*. Of the long-chain saturates, 18:0 was more strongly represented in the phospholipids (>6%) of both species, and so too is 22:0 and 24:0 in *E. vallentini* and *E. similis* v. *armata* respectively.

The dominant monounsaturated fatty acids in both species are 16:1(ω7), 18:1(ω9) and 18:1(ω7). The ratio 18:1(ω9)/18:1(ω7) is < 1 for *E. similis*, but >1 for *E. vallentini*. This ratio is believed to be an indication of the balance between exogenous and *de novo* sources of lipid. Long-chain monounsaturates, 20:1, 22:1 and 24:1, occurred only in very low concentrations, as they do in *E. superba* (Clarke 1980). Polyunsaturates were represented by 20:4(ω6), 20:5(ω3), and 22:6(ω3). *E. vallentini* was richer in these polyunsaturates than *E. similis* v. *armata*.

Differences in the fatty acid composition of phospholipid and triacylglycerol are not substantial. For both species the unusual polyunsaturate 21:5(ω2) occurred only in the phospholipids, though in small amounts. Free fatty acid composition, however, did differ from that of phospholipid and triacylglycerol in *E. vallentini* by having more saturates, but in *E. similis* v. *armata* by having more polyunsaturates, in particular 22:5(ω3) and 22:6(ω3).

The stomachs of 7 specimens of *E. vallentini* were dissected out and opened to estimate stomach fullness and gut contents. Table 7 lists these findings. Finely particulate unidentified matter was interpreted as detritus.

Nematoscelis megalops

About 60% of the lipid of this species consisted of phospholipids, and only a trace of triacylglycerol was present. Correspondingly, the total lipid content was only 1.5% of wet mass. Partial glycerides constituted 17% of total lipid.

Table 6. Fatty acid composition of the lipid classes of *Euphausia vallentini* and *E. similis* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids which constitute >1% of the total are listed. Blanks indicate absence.

	Phospholipid	Free Fatty Acid	Triacylglycerol
		Euphausia vallentini	
14:0	4.7	13.6	4.9
15:0		2.9	1.2
16:1	3.6	6.5	2.8
16:0	23.4	35.0	21.7
18:4			3.2
18:2			2.7
18:1(ω9)	12.2	9.6	9.7
18:1(ω7)		1.9	4.6
18:0	11.6	9.9	1.7
20:4(ω6)		2.2	1.6
20:5(ω3)	10.3	2.8	19.5
21:5	1.7		
22:6(ω3)	12.4	2.0	17.9
22:0	2.8	4.9	0.4
Total unknown of >1% occurrence	2.4		
		Euphausia similis	
14:0	4.8	2.9	14.2
15:0	1.3	0.8	2.0
16:1	0.8	1.9	2.4
16:0	17.7	14.4	24.5
18:4	1.0	2.5	2.0
18:2	9.8	2.4	3.7
18:1(ω9)	5.3	6.8	6.1
18:1(w7)	6.6	3.5	10.9
18:0	6.4	0.7	2.9
20:4(ω6)	2.3	1.8	
20:5(ω3)	2.2	21.7	0.2
21:5	1.2		
22:6(ω3)	3.1	24.7	1.5
24:1	1.1		
24:0	1.6		
Total unknown of >1% occurrence	16.0	6.9	11.6

Table 7: Stomach fullness and gut contents of *Euphausia vallentini*. Stomach fullness index: 0 = empty, 1 = 1/4 full, 2 = 1/2 full, 3 = 3/4 full, 4 = full. Stomach content index: blank = absent, 1 = present, 2 = abundant, 3 = very abundant.

Date, time, position	Size mm	Stomach fullness	Stomach composition				
			Diatoms	Foraminifera	Tintinnids	Radiolarians	Detritus
23-04-1989,	18.5	3	1				3
19h30,	20.2	3	1	2	1	1	3
46°48'S,38°00'E	20.0	3		2		1	3
24-04-1989,	19.5	4	1	2			3
01h30,	17.0	3		2			3
46°49'S,38°01'E							
24-04-1989,	19.0	3		2	1		3
04h30,	16.5	4		2			3
46°49'S,38°0'E							

Table 8 lists the fatty acid composition of the phospholipid and free fatty acid fractions. Again the saturates of phospholipid are represented most strongly by 16:0, but also 14:0 and 18:0. The ω7 monounsaturate levels are low (<5%) compared to that of the 18:1(ω9) isomer (14%). The presence of the unusual 22:1(ω11) isomer is more than likely of copepod origin (Pascall and Ackman 1976, Sargent and Henderson 1986). Polyunsaturates were dominated by long-chain ω3 isomers.

The free fatty acid composition differed in having proportionately more saturated than polyunsaturated fatty acids. The strong presence of 12:0 (30%) in the free fatty acids is unusual, and might be due to a contaminant. A large number of unidentified substances accounted for 28.2% of the free fatty acids.

***Thysanoessa* spp.**

T. vicina and *T. macrura* specimens were late juveniles. *T. gregaria* specimens were all adults. Significant fractions of the lipid of *T. vicina* and *T. macrura* (30% and 8% respectively) were in the form of wax ester, while only a trace of wax ester was found in *T. gregaria*. Triacylglycerols were less important, except in *T. gregaria*. Free fatty acids (including, perhaps, fatty alcohols) were major components in all three species. None of the species were particularly rich in total lipids (2.8-3.4% wet mass).

The fatty acid composition of the phospholipid, free fatty acid and wax ester fractions of *T. vicina* are listed in table 9. These fatty acids were principally the saturates, 14:0 and 16:0, the monounsaturates 16:1(ω7), 18:1(ω7) and 18:1(ω9), and ω3 polyunsaturates. The ratio of 18:1(ω7):18:1(ω9) exceeded 1 in both the phospholipid and the wax ester. Longer-chained saturated and monounsaturated fatty acids were absent.

***Metridia* spp.**

M. gerlachei and *M. lucens* were rich in wax ester (50% and 26% total lipid respectively) and triacylglycerol (18% and 48% total lipid respectively). The 12% free fatty acid content of *M. gerlachei* might include fatty alcohols as these two substances did not separate clearly. The relatively low phospholipid content is a reflection of the higher total lipid content of these two

Table 8: Fatty acid composition of the phospholipids and free fatty acids of *Nematoscelis megalops* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids which constitute >1% of the total are listed. Blanks indicate absence.

	Phospholipid	Free fatty acid
12:0	0.5	30.8
14:0	3.2	1.6
15:0	1.0	
16:1	4.0	2.5
16:0	25.2	4.1
18:4	0.6	
18:2	1.8	
18:1(ω9)	13.6	2.9
18:1(ω7)	3.2	
18:0	3.3	1.3
20:4(ω6)	1.3	
20:5(ω3)	12.2	
21:5	0.2	
22:6(ω3)	16.5	
22:1(ω11)	2.0	
Total unknown of >1% occurrence	1.6	28.2

Table 9: Fatty acid composition of the lipid classes of *Thysanoessa vicina* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids which constitute >1% of the total are listed. Blanks indicate absence.

	Phospholipid	Free Fatty Acid	Wax Ester
14:0	6.3	2.1	6.2
15:0	0.2	1.0	
16:1(ω7)	11.8	1.0	8.5
16:0	26.2	18.2	23.8
18:4(ω3)	1.2	1.0	0.8
18:2(ω6)	2.0	2.1	3.1
18:1(ω9)	7.3	7.1	8.2
18:1(ω7)	10.4	2.5	11.1
18:0	1.1	2.0	2.2
20:5(ω3)	12.9	17.3	14.9
22:6(ω3)	16.7	20.8	0.5
Total unknown of >1% occurrence	3.6	19.5	0.9

copepods; *M. gerlachei* contained 14% lipid (wet mass) wheras *M. lucens* contained 6.7% lipid.

The fatty acid composition of the free fatty acids, triacylglycerols and wax esters of *M. gerlachei* are listed in table 10. Due to the low levels of phospholipids, and the small sample of oil available for analysis, the phospholipid content could not be analysed with confidence. The neutral lipids were rich in saturates, again 16:0 dominating. The monounsaturates were dominated by the ω9 isomer in all three lipid classes. Long-chain monounsaturates, 20:1(ω9), 22:1(ω11) and 24:1(ω13), were present, but in low concentrations. Polyunsaturates were dominated in the neutral lipid by the ω3 isomer of 20:5 and 22:6.

Discussion

The strong presence of free fatty acids in many of the species examined could be due to deterioration of lipids after death (autolysis) or due to metabolic break down of lipids prior to death. According to temperature dependent rates of hydrolysis of phospholipids and neutral lipids in hake (*Merluccius capensis*) (De Koning and Mol 1989), at -80°C free fatty acid is formed at a rate of 0.00023 mmoles kg^{-1} day^{-1} from phospholipid and 0.0073 mmoles kg^{-1} day^{-1} from neutral lipid. For a mixture of 60% phospholipid and 40% neutral lipid, 0.0031mmoles free fatty acid are formed per kg lipid per day (or 0.87 oleic acid kg^{-1} day^{-1}). In 1000 days this amounts to < 0.01% autolysis. As this rate decreases exponentially with temperature, at -80°C the rate of free fatty acid formation while in storage should have been negligible. Some autolysis might have occurred in the freshly caught animals while these were being identified, as autolysis in freshly caught krill can proceed rapidly (Eddie 1977). Nonetheless, the possibility that an absence of wax ester, or of triacylglycerol, in certain species is due to deterioration can be discounted, since some species contained an abundance of these lipid classes, and all specimens were treated in the same way. The high free fatty acids in some species might simply reflect a paucity of neutral lipid, and it is likely that this result reflects a condition prior to death. As with the

Table 10. Fatty acid composition of the lipid classes of *Metridia princeps* caught at the Prince Edward Islands, April/May 1990. Only those fatty acids which constitute >1% of the total are listed. Blanks indicate absence.

	Free Fatty Acid	Triacylglycerol	Wax Ester
14:0	4.2	6.4	2.9
15:0		0.6	0.3
16:4		1.1	0.7
16:1(ω7)	4.4	5.0	10.6
16:0	18.2	21.2	9.3
18:4	1.9	1.5	2.6
18:2	2.1	1.1	1.4
18:1(ω9)	10.4	7.0	24.9
18:1(ω7)	2.2	4.4	1.6
18:0	4.2	4.2	2.0
20:4(ω6)	0.6	0.5	0.6
20:5(ω3)	15.1	11.7	13.0
20:1	1.6	2.2	1.1
22:6(ω3)	16.6	7.3	9.0
22:5	1.6	1.7	1.5
22:1(ω11)	1.1	3.7	0.6
24:1	1.7	0.8	0.5
Total unknown of >1% occurrence	11.3	4.9	1.3

free fatty acids, the interpretation of high levels of partial glycerides might be ambiguous, though the concentrations are greatest for the lipid poor pecies.

The fatty acid composition of phospholipid is understood to be less variable than that of neutral lipid, which might be attributable to the specific functional role of phospholipid as a structural element (Clarke 1980). Indicators of diet should thus be sought among the fatty acids of neutral lipid. Phytoplankton is known to be rich in 14:0, 16:0, 16:1(ω7) and ω3 polyunsaturates (Sargent et al. 1985). These featured strongly in the triacylglycerols and free fatty acids of the four *Euphausia* species and particularly in the wax ester and triacylglycerol of *Thysanoessa vicina* and *Metridia gerlachei*, suggesting a phytoplanktonic diet for these species. Considering the paucity of long-chain saturated or monounsaturated fatty acids, likely to have been derived from the alcohol moiety of crustacean prey wax ester, the four species examined (*E. vallentini, E. similis v. armata, T. vicina* and *M. gerlachei*) were likely to have been herbivorous in the preceeding summer months. Of these, it might be expected that the *Euphausia* species at least, being rather poor in lipid, would turn to an alternative winter diet. Given a lack of neutral lipid in *Nematoscelis megalops*, nothing can be interpretatied of its diet, though the phytoplankton fatty acids are abundant in the phospholipids.

In all the specimens examined, except *E. similis* v. *armata* and *T. vicina*, the ω9 isomer of 18:1 predominated, suggesting that carnivory may be an important source of this isomer. Alternatively, domination of the ω9 isomer could be a result of considerable *de novo* synthesis of lipid despite a phytoplanktonic input of the ω7 isomer. This interpretatation is thus ambiguous.

Mauchline's (1980) review of the biology of the euphausiids lists the known dietery items of several species. *T. gregaria* is listed as a filter-feeder/omnivore; *Nematoscelis megalops* is listed as an omnivore/predator; *E. similis* is known to eat coccolithophores and tintinids, though this list is surely incomplete. Nothing has been documented on the diet of other sub-Antarctic species. Diatoms, foraminifera, tintinids and radiolarians were found in the stomachs of the 7 specimens of *E. vallentini* examined. *M. gerlachei* shows great

efficiency at handling large size diatoms (46μm) (Schnack 1983). Based on 'edge-indices' of the mandibles, this species is a potential omnivore.

Compared to records from the Antarctic, the lipid content of the *Euphausia* spp. examined in this study (1.3 - 2.8%) was low. For mature *E. superba*, *E. frigida* and *E. triancantha* the known lipid contents are 5-8%, 19.4% and 4% respectively (Clarke 1980). However, compared to tropical and warm-temperate species these low levels are normal; *E. americana* and *E. krohni* from 20°N had 0.8% and 1.0% lipid (Morris 1971), *E. pacifica* had 3.1% lipid off southern California (Childress and Nygaard 1974), *E. gibboides* from 22°N and 28°N had 1.2% lipid (Morris 1971) and *E. similis* off Japan had 2.1% lipid (compared to 2.8 for *E. similis* v. *armata* from this study). The mature *T. gregaria* (3.4% lipid) can be compared to its north Atlantic congeners *T. inermis* (7-8% lipid) and *T. raschii* (18% lipid) (Hopkins et al. 1984) and the north Pacific congener *T. longiceps* (7.7%) (Sameoto et al. 1975). The equally low lipid contents of *T. vicina* and *T. macrura* late juveniles might, however, be more typical of immature *Thysanoessa* specimens (Hopkins et al. 1984). *Metridia gerlachei* had 14.1% lipid, and *M. lucens* 6.7%, which is similar to autumn values for *M. longa* from the Arctic 11.5% (assuming that dry mass = 0.2 wet mass) (Lee 1975) and to *R. gigas* from the Antarctic 13.8% (Lee and Hirota 1973).

Figure 11 shows the known latitudinal distributions of the species in this study. No species occurs at both the Sub-tropical Convergence (STC) and the Antarctic Polar Front (APF), as might be expected from the strong temperature gradient. *E. vallentini* can be considered as a sub-Antarctic species which occurs over the APF. *E. similis* v. *armata* and *E. longirostris* are also common in the sub-Antarctic, but their distributions clearly overlap the STC. *N. megalops* is common between 30° and 45° in both hemispheres. The *Thysanoessa* spp. show a clear geographical seperation; *T. gregaria* is subtropical, *T. vicina* is Antarctic/sub-Antarctic, *T. macrura* is high Antarctic (Nemoto 1966). *M. lucens* is abundant in sub-Antarctic water between Marion and Crozet islands, and also appears in the cold upwelled water of the Benguela current in the south east Atlantic (De Decker 1984). *M. gerlachei* is a common Antarctic species (Raymont 1983). The presence of Antarctic and subtropical elements in sub-Antarctic water can be explained by the interaction of the west

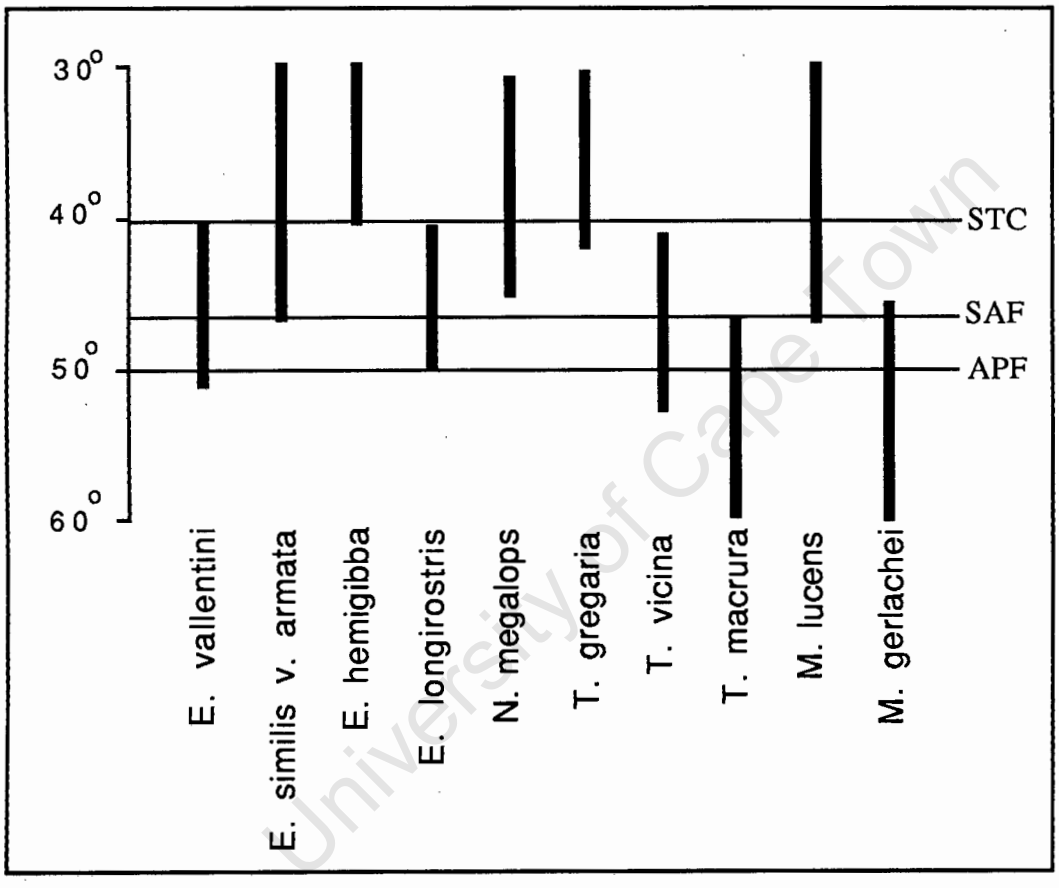

Figure 11: The known distribution of the ten zooplankton species in the southern Indian ocean considered in this study. The information comes from Boden (1954), Mauchline and Fischer (1964), Nemoto (1966), Raymont (1983), De Decker (1984).

wind drift with the irregular bottom topography in these longitudes, which causes a mixing of surface waters across the circumpolar fronts (Deacon 1983).

The low lipid content observed in many of the sub-Antarctic species may perhaps be explained by the poor feeding conditions encountered in this biogeographic region. Chlorophyll a measured at 89 stations on the same cruise of the M.V. S.A. Agulhas (April/May) did not exceed 0.4 mg Chl a $.m^{-3}$ over five weeks (mean 0.19 mg Chl a $.m^{-3}$) at least 50% of which was in the picoplankton size fraction (< 2.0 μm). Though the mid-summer chlorophyll-*a* values might be expected to be higher, a synthesis of data collected on 11 Japanese Antarctic Research Expedition (JARE) voyages from Fremantle to the Japanese Antarctic base (Syowa) in early summer and the return voyages to Cape Town in mid/late summer (figure 12) show that the average Chlorophyll-*a* concentration in the sub-Antarctic region, 45-49°S, of the Indian ocean in summer is low and invariable when compared to the STC and to the APF. The weak and poorly understood sub-Antarctic Front (SAF) (Lutjeharms et al. 1985) is seldom associated with elevated chlorophyll concentrations. No data are available to compare the winter situation. I would presume however that in winter chlorophyll is scarce due to low light levels south of the APF, and both poor light and unstable water between the STC and APF. Both sub-Antarctic and Antarctic zooplankton are 5-6 times more abundant, measured volumetrically, in summer than in winter (Foxton 1956). A moderate winter north of the STC would afford this region some winter production. The sub-Antarctic region, integrated over a period of one year, is perhaps the least productive area within the respective ranges of the species under consideration. The frontal zones either side of the sub-Antarctic are far more productive. Correspondingly, the zooplankton biomass in the sub-Antarctic is 2-3 times lower than that of the APF and further south, but not less than the tropical water to the north (Foxton 1956, Vladimirskaya 1976).

Although a low lipid content (1-3% wet weight) might be normal for (sub)tropical euphausiids, the sub-Antarctic is not subtropical but strongly seasonal. Such low values for the end of summer would suggest that the species examined in this study would feed carnivorously on organisms with a long generation time which persist during winter. Alternatively, the subtropical species were too far south to maintain a herbivorous diet in

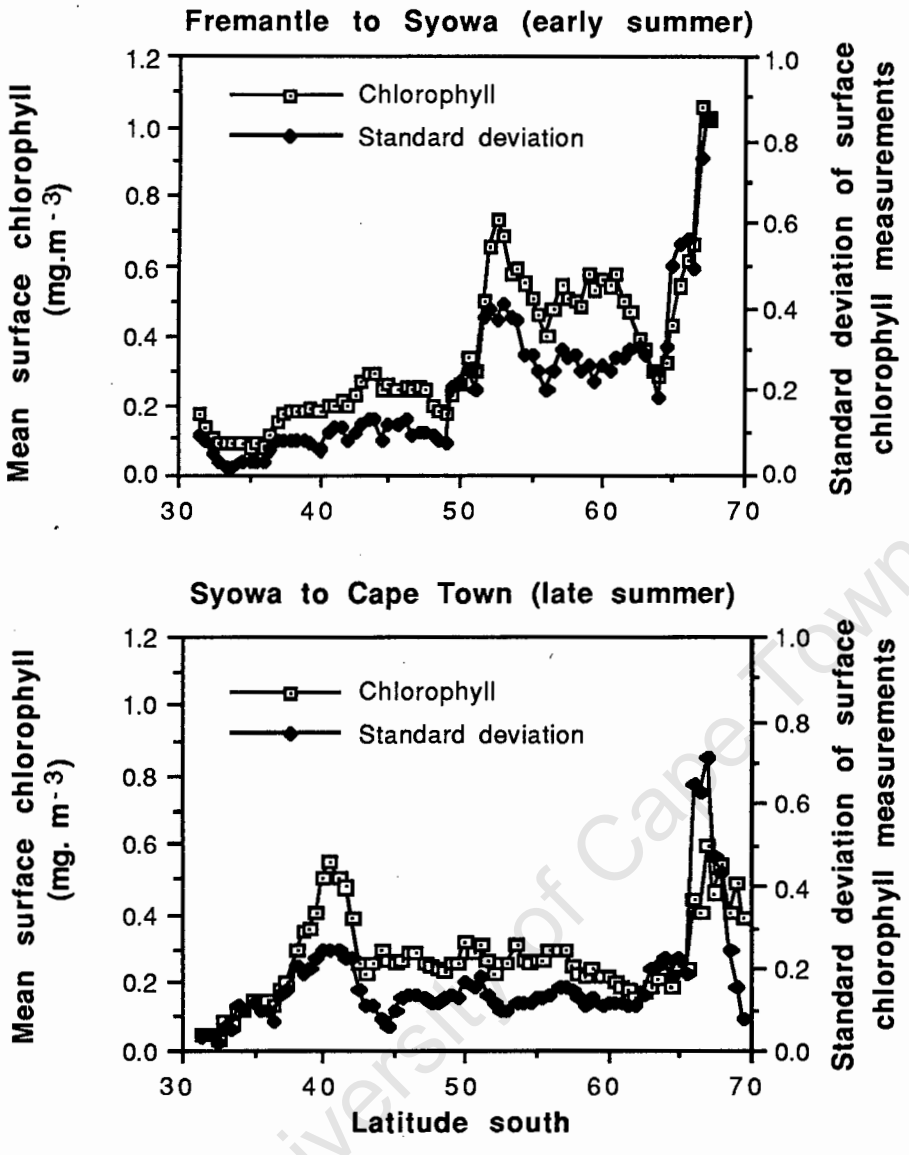

Figure 12: A synthesis of surface chlorophyll-a measurements taken on 11 cruises from Fremantle to Syowa (68°22'S; 44°08'E) in the months December and January, and again from Syowa to Cape Town in the months February and March. The data points are means for each half degree, but smoothed with a running mean spanning 1.5°. Data comes from Tominaga (1971), Nishiwaki (1972), Hoshino (1974), Ohyama and Mayama (1976), Ohno (1976), Fukuchi (1977), Kuroda (1978), Tanimura (1981), Yamagata and Fukui (1981), Fukuchi and Tamura (1982) and Watanabe and Nakajima (1983).

winter. In the case of the Antarctic species, *T. vicina* and *T. macrura*, these specimens might have been too far north to accumulate a large lipid store for winter, as other polar herbivorous species generaly have >10% of wet weight as lipid at the close of summer. The two copepod species were richer in lipid and it is possible that these harvest the available phytoplankton more efficiently, perhaps by selecting smaller algae. Coccolithophores, radiolarians and tintinnids do seem to constitute a significant fraction of euphausiid diet. Microzooplankton might provide a better food source where phytoplankton are dominated by the pico-size fraction as many euphausiids cannot filter small particles (< 5 μm) efficiently (Boyd et al. 1984; Quetin and Ross 1985, Stuart 1989). Unfortunately the seasonal availability, nutritional contibution and lipid characteristics of these protozoans are unknown.

The lack of wax ester in the *Euphausia* spp., *Nematoscelis megalops* and *T. gregaria* indicates that no rapid synthesis of neutral lipid occurred in preparation for a non-feeding winter in these species. This situation is the same as that for *E. superba*, which is omnivorous. *T. vicina* and *T. macrura* both stored wax esters in contrast to *T. gregaria* which is a subtropical species. Similarly *M. gerlachei* of Antarctic affinity stored more wax ester than *M. lucens* of a more temperate distribution. These latitudinal differences fit the hypothesis of Lee et al. (1971), and these wax ester storing species could be entirely herbivorous.

Thysanoessa vicina and *T. macrura* are the dominant prey items of penguins from Marion Island and Gough Island (Williams and Laycock 1981). Three representative species of the sea-bird community at Marion, a penguin, an albatross and a petrel, are able to rapidly digest wax ester and triacylglycerols (Jackson and Place, in press). If the *Thysanoessa* prey species are indeed herbivorous, then these tertiary predators end a rather short food chain (plant - herbivore - bird) in an oceanic environment which is traditionally expected to be characterised by long food chains (Ryther 1969). I acknowledge, however, that the role of microzooplankton as an intermediate step between pico-phytoplankton and zooplankton may be critically important in the chlorophyll-poor waters of the sub-Antarctic.

References

Bligh, E.G.and W.J. Dyer (1959) A rapid method of total lipid extraction and purification. *Can. J. Biochem. Physiol.*, 37, 911-917.

Boden, B.P. (1954) The euphausiid crustaceans of southern African waters. *Trans. R.Soc. S. Afr.*, 34, 181-243.

Bottino, N.R. (1974) The fatty acids of Antarctic phytoplankton and Euphausiids. Fatty acid exchange among trophic levels of the Ross Sea. *Mar. Biol.*, 27, 197-204.

Boyd, C.M., M. Heyraud and C.N. Boyd (1984) Feeding of the Antarctic krill *Euphausia superba*. *J.Crust. Biol.*, 4(1), 123-141.

Childress, J.J. and M. Nygaard (1974) Chemical composition and buoyancy of midwater crustaceans as function of depth of occurrence off southern California. *Mar. Biol.*, 27, 225-238.

Clarke, A. (1980) The biochemical composition of krill, *Euphausia superba* Dana, from South Georgia. *J. Exp. Mar. Biol. Ecol.*, 43, 221-236.

Deacon, G E.R. (1983) Kerguelen, Antarctic and subAntarctic. *Deep-Sea Res.*, 30(1), 77-81.

De Decker, A H.B. (1984) Near-surface copepod distribution in the south-western Indian and south-eastern Atlantic ocean. *Ann. S. Afr. Mus.*, 93(5), 303-370.

De Koning, A.J.and T.H. Mol (1990) Rates of free fatty acid formation from phospholipids and neutral lipids in frozen cape hake (*Merluccius* spp) mince at various temperatures. *J. Sci. Food Agric.*, 50, 391-398.

Eddie, G.O. (1977) The harvesting of krill. Rome, Food and Agriculture Organisation of the United Nations, United Nations Development programme, Southern ocean Fisheries Survey Programme GLO/SO/77/1.

Falk-Peterson, S., R.R. Gatten, J.R. Sargent and C.C.E. Hopkins (1981) Ecological investigations on the zooplankton community of Balsfjorden, northern Norway. Seasonal changes in the lipid class composition of *Meganyctiphanes norvegica*

(M.Sars), *Thysanoessa raschii* (M. Sars) and *T. inermis* (KrØyer). *J. exp. mar. Biol. Ecol.*, 54, 209-224.

Falk-Petersen, S., J.R. Sargent and K.S. Tande (1987) Lipid composition of Zooplankton in relation to the Sub-Arctic food web. *Pol. Biol.*, 8, 115-120.

Foxton, P. (1956) The distribution of the standing crop of zooplankton in the Southern Ocean *Disc. Rep.*, 28, 193-258.

Fukuchi, M. (1977) Chlorophyll-*a* content in the surface water along the course of the Fuji to and from Antarctica in 1976-1977. *Polar Rec.*, 60, 57-69.

Fukuchi, M. and S.Tamura (1982) Chlorophyll-*a* distribution in the Indian sector of the Antarctic Ocean in 1978-1979. *Polar Rec.*, 74, 143-162.

Harwood, J.L. and N.J. Russell (1984) Lipids in plant and microbes. George Allen and Unwin, London.

Hopkins, C.C.E., K.S. Tande and S. Gronvik (1984) Ecological investigations of the zooplankton community of Balsfjorden, Northern Norway: An analysis of growth and overwintering tactics in relation to niche and environment in *Metridia longa* (Lubbock), *Calanus finmarchicus* (Gunnerus), *Thysanoessa inermis* (Kroyer) and *T. raschi* (M. Sars). *J. exp. mar. Biol. Ecol.*, 82, 77-99.

Hoshino, T. (1974). Surface water Chlorophyll-*a* contents observed during the cruise of the Fuji to Antarctica, November 1973-April 1974. *Polar Rec.*, 51, 29-38.

Jackson, S., and A. R. Place (in press) Gastrointestinal transit and lipid assimilation efficiencies in three species of sub-Antarctic seabird. *J. Exp. Zool.*

Kattner, G., and M. Krause (1987) Changes in lipids during the development of *Calanus finmarchicus* s.l. from copepodid I to adult. *Mar. Biol.*, 96, 511-518.

Kuroda, K. (1978) Distribution of chlorophyll-*a* contents in the surface water along the course of the Fuji to and from Antarctica in 1972-1973. *Polar Rec.*, 61, 65-74.

Lee, R.F., J. Hirota and A.M. Barnett (1971) Distribution and importance of wax esters in marine copepods and other zooplankton. *Deep-Sea Res.*, 18, 1147-1165.

Lee, R.F. (1974) Lipid composition of the copepod *Calanus hyperboreus* from the Arctic ocean. Changes with depth and season. *Mar. Biol.*, 26, 313-318.

Lee, R.F. (1975) Lipids of arctic zooplankton. *Comp. Biochem. Physiol.*, 52B, 263-266.

Lee, R.F. and J. Hirota (1973) Wax esters in tropical zooplankton and nekton and the geographical distribution of wax esters in marine copepods. *Limnol. Oceanogr.*, 18, 227-239.

Lutjeharms, J.R.E., N.M. Walters and B.R. Allanson (1985). Oceanic frontal systems and biological enhancement. In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried, P.R. Condy and R.M. Laws, editors, Springer-Verlag, Berlin, pp. 11-21.

Mauchline, J. and R. Fisher (1964) The biology of the euphausiids. *Adv. Mar. Biol.*, 7, 1-454.

Mauchline, J. (1980) The biology of mysids and euphausiids. *Adv. Mar. Biol.*, 18, 1-681.

Morris, R.J. (1971) Variations in the fatty acid composition of oceanic euphausiids. *Deep-Sea Res.*, 18, 525-529.

Nemoto, T. (1966) *Thysanoessa* euphausiids, comparative morphology, allomorphosis and ecology. *Scient. Rep. Whales Res. Inst*, Tokyo, 20, 109-155.

Nishiwaki, S. (1972) Chlorophyll-*a* content in the sea surface water observed in 1970-1971 during the cruise of Fuji to Antarctica. *Pol. Record*, 44, 93-99.

Ohman, M.D. (1988) Sources of variability in measurements of copepod lipids and gut fluorescence in the California current coastal zone. *Mar. Ecol. Prog Ser.*, 42, 143-153.

Ohno, M. (1976) Chlorophyll-*a* content in the surface water observed during the cruise of the Fuji to Antarctica in 1974-1975. *Polar. Rec.*, 57, 106-114.

Ohyama, Y. and T. Mayama (1976) Chlorophyll-*a* contents in the surface water observed during the relief voyage of Fuji to Syowa Station, Antarctica, in 1975-1976. *Polar Rec.*, 57, 115-122.

Pascall, J.C. and R.G. Ackman (1976) Long chain monoethylenic alcohol and acid isomers in lipids of copepods and capelin. *Chem. Phys. Lipids.*, 16, 219-223.

Pillar, S.C. and V. Stuart (1988) Population structure, reproductive biology and maintenance of *Euphausia lucens* in the southern Benguela current. *J. Plank. Res.*, 10(6), 1083-1098

Prahl, F.G., G. Eglinton, E.D.S. Corner, S.C.M. O'Hara, and T.E.V. Forsberg (1984) Changes in the plant lipids during tpassage through the gut of *Calanus*. *J. mar. biol. Assoc. U.K.*, 64, 317-334.

Price, H.J., K.R. Boyd and C.M. Boyd (1988) Omnivorous feeding behaviour of the Antarctic krill *Euphausia superba*. *Mar. Biol.*, 97, 67-77.

Quetin, L.B. and R. M. Ross (1985) Feeding by Antarctic krill, *Euphausia supeba*: does size matter? In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried, P.R. Condy and R.M.Laws, Springer-Verlag, Berlin, 372-377.

Raymont, J.E.G. (1983) Plankton and Productivity in the Oceans. Volume 2 Zooplankton. Pergamon Press, Oxford.

Ryther, J.H. (1969) Photosynthesis and fish production in the sea. *Science* 166, 72-76.

Sameoto, D.D., D.C. Darrow and S.Guildford (1975) DDT residues in the upper estuary of the Gulf of St. Lawrence. *J. Fish. Res. Bd. Can.*, 32, 310-314.

Sargent, J.R., H.C. Eilertsen, S. Falk-Petersen, and J.P. Taasen (1985) Carbon assimilation and lipid production in phytoplankton in northern Norwegian fjords. *Mar. Biol.*, 85, 109-116.

Sargent, J.R. and S. Falk-Petersen (1981) Ecological investigations on the zooplankton community in Balsfjorden, Northern Norway: Lipids and fatty acids in *Meganyctiphanes norvegica, Thysanoessa raschi* and *T. inermis* during mid-winter. *Mar. Biol.*, 62, 131-137.

Sargent, J.R. and R.J. Henderson (1986) Lipids. In: *The biological chemistry of Marine copepods*, E.D.S. Corner and S.C. O'Hara, editors, Clarendon Press, Oxford.

Sargent, J.R. and R. McIntosh (1974) Studies on the mechanism of biosynthesis of wax esters in *Euchaeta norvegica*. *Mar. Biol.*, 25, 271-277.

Schnack, S.B. (1983) Feeding of two Antarctic copepod species (*Calanus propinquus and Metridia gerlachei*) on a mixture of centric diatoms. *Polar Biol.*, 2, 63-68.

Smith, A.E. and I. Morris (1980) Synthesis of lipid during photosynthesis by phytoplankton of the Southern Ocean. *Science*, 207, 197-199.

Stuart, V. (1989) Observations on the feeding of *Euphausia lucens* on natural phytoplankton suspensions in the southern Benguela upwelling region. *Cont. Shelf. Sci.*, 9(11), 1017-1028.

Tanimura, A. (1981) Distribution of the surface chlorophyll-*a* along the course of the Fuji to and from Antarctica in 1979-1980. *Polar Rec.*, 72, 35-42.

Tominaga, H. (1971) Chlorophyll-*a* and Phaeophytin contents in the surface water of the Antarctic ocean through the Indian Ocean. *Polar Rec.*, 42, 124-134.

Wagener, W.W.D., C.K. Simmonds and M. Stemmet (1984) Ten individual analyses by gas chromatography of a fish oil for fatty acid content: establishng the repeatability of results. Fishing Industry research Institute, Thirty-eighth annual report of the director, University of Cape Town.

Watanabe, K. and Y. Nakajima (1983) Surface distribution of Chlorophyll-*a* along the course of the Fuji (1980/81) in the Southern Ocean. *Polar Rec.*, 77, 33-39.

Willason, S.W., J. Favuzzi and J.L.Cox (1986) Patchiness and nutritional condition of zooplankton in the California Curent. *Fish. Bull.*, 84(1), 157-176.

Williams, A.J. and P.A. Laycock (1981) Euphausiids in the diet of some sub-Antarctic *Eudyptes* penguins. *S. Afr. J. Antarct. Res.*, 10/11, 27-28.

Vladimirskaya, Ye. V. (1976) Distribution of zooplankton in Scotia Sea in fall and winter. *Oceanology*, 15, 359-362.

Yamagata, K. and F. Fukui (1981) Chlorophyll-*a* content in the Indian sector of the Antarctic Ocean. *Polar. Rec.*, 73, 72-81.

Chapter 3

Production and standing stocks of the kelp *Macrocyctis laevis* Hay

Abstract-The recently described species *Macrocystis laevis* Hay is endemic to the Prince Edward Islands. Aerial photographs of Marion Island were used to outline the distribution of the kelp and to assess its cover. *M. laevis* occurs along the lee shore of the island, between the 5 and 20m isobaths. Plant densities and gross plant morphology were measured by divers during April/May 1988. Net production was estimated from growth measurements taken in April/May 1988 and 1989 and again during August 1989. The mean biomass of kelp was 0.67 $kgC.m^{-2}$ within the kelp beds. Net production is estimated at 7.7 $gC.m^{-2}.d^{-1}$ and 11.5 $gC.m^{-2}.d^{-1}$ during the months of April and August respectively. *M. laevis* had a uniform frond-length frequency distribution, which suggests that only the oldest fronds are lost by wave action or senescence. Based on calculations for *M. laevis* and *Durvillea antarctica* (the two species making up most of the macrophyte biomass) macrophytes are more productive per unit area than the phytoplankton but contribute less to the seas around the Prince Edward Islands by virtue of their small spatial coverage. Neither of the kelps lose much material as particulate or dissolved organic carbon through fragmentation. The extent of grazing on live *M. laevis* fronds is unknown, and only *D. antarctica* contributes to a macrofaunal detrital community. The contribution of *M. laevis* production to the nearshore ecology of the islands seems limited, as I suspect that almost all of its production is exported to the open ocean pelagic system.

Introduction

The sub-Antarctic Marion and Prince Edward Islands (46°54'S; 37°45'E) harbour the recently described species *Macrocystis laevis* Hay, which as yet has not been recorded elsewhere. This makes *M. laevis* the most localised of the four species of *Macrocystis*. *M. laevis* had previously been confused with the giant kelp *M. pyrifera*, but differs in having entirely smooth vesiculate blades. *M. pyrifera* is widespread, occurring on the western seaboard of north America, in south America beyond 44°S, and on the shores of the sub-Antarctic islands of Gough, Tristan da Cuñha, Kerguelen and Crozet, New Zealand and Tasmania (Mann 1973). Hay (1986) discussed the possibility that *M. laevis* arrived at the Prince Edward Islands via the west wind drift from a smooth-bladed population at South America, now extinct or unlocated. Such a population was recorded early this century at the Falkland Islands (Skottsberg 1921).

Like *M. pyrifera*, *M. laevis* grows to a length of < 20m in dense forests in sheltered water of less than 20m depth. At present nothing is known of the ecology of *M. laevis*, though we could reasonably expect a strong similarity with that of the more cosmopolitan *M. pyrifera*.

The ecology of several populations of *M. pyrifera* has been investigated with respect to the key biotic and physical structuring processes. The most notable description of biotic interactions with *M. pyrifera*, namely the ability of sea urchins to 'overgraze' kelp forests and the role of keystone predators in controlling urchin densities, came from the Californian kelp forests (Leighton et al. 1966, Chapman 1981). A search for a parallel in the south American populations has proven largely unsuccessful (Castilla and Moreno 1982, Santelices and Ojeda 1984a), though Dayton (1985) does describe severe grazing pressure by the urchin *Loxechinus albus* in certain areas. Castilla's (1985) hypothesis predicts that in the absence of considerable predation on urchins or other herbivores, herbivory is unlikely to be a significant factor if the kelp forests are to persist in time. The simplistic nature of the southern American kelp communities, by comparison with those of the northern hemisphere,

is ascribed to the effect of ice scouring the coast during the Pleistocene, with recolonization occurring only since that period (Dayton 1985).

Delépine (1976) provided a description of *M. pyrifera* from Kerguelen Island and more recently Van Tussenbroek (1989) has described the seasonal growth of *M. pyrifera* fronds from the Falkland Islands. It is these southern ocean populations of *Macrocystis pyrifera* with which can be compared *M. laevis*, as they both occur in the sub-Antarctic water mass and are biogeographically linked by the west wind drift.

The dominant biotic interaction of the south American populations seems to be with other macrophytic species, resulting in clearly defined algal zonation. The criterion determining the replacement of *Macrocystis* at the shallow extent is its intolerance to wave action, whilst at the deeper extent diminished light availability favours other species. Nonetheless, differences in algal communities at various locations where *Macrocystis* occurs means that this species does not always occupy the same depth zone. At South America alone the shallow limits of the zonation of *M. pyrifera* vary from 1 to 5 m depth, whilst the deep extremes vary from 5 to 25 m (Santelices and Ojeda 1984b, Dayton 1985). The simulation model developed by Jackson (1987) predicts that the production and the number of fronds per plant is, at least in part, a function of the water depth.

The other important forcing function altering growth is the photoperiod. At extreme latitudes (>60°) the shortened photoperiod during winter results in a negative growth rate and the plants fail to survive the winter, despite extended light availability in the summer. A strong seasonal trend in the growth of *M. pyrifera* fronds has been described at the Falkland Islands (52°S). At 47°S the Prince Edward Islands appear to be well within the latitudinal range of *Macrocystis*, though seasonal differences in the production of *M. laevis* are to be expected.

The Prince Edward Islands support a large biomass of birds (±2.0 x 10^7kg, Adams 1990). It has been suggested that this is supported by enriched production in the Prince Edward Island Seas, a phenomenon described as an island mass effect (El Sayed et al. 1976, Boden 1988, Perissinotto et al., 1990). Certainly as regards phytoplankton production, there does appear to be considerable local enhancement, though the exact mechanism is still

unclear. The shelf around the islands is covered with a rich, predominantly filter-feeding, benthic community. Of some interest are the sources of food to these communities and the relative importance of phytoplankton, kelp (both *Macrocystis* and *Durvillaea*) and introduced material.

This paper is a synthesis of the first measurements made on *M. laevis*, on three cruises to the Prince Edward Islands during April/May 1988, April/May 1989 and August 1989. The aim of this work is to investigate aspects of the ecology and production of *M. laevis*, and to assess the role of kelp in the ecology of the islands. Measurements included growth rates, forest density and cover, and gross plant morphology.

Methods

The rate of frond growth was determined by measuring the length increment in the apical 2 m. Each frond consists of a rope-like stipe with blades attached along its length. Individual fronds were marked by loosely clamping 10 mm diameter plastic and aluminium bird rings to fronds at either 1 m or both 1 m and 2 m from the growing tip. Only fronds with intact terminal blades were selected for growth experiments. After a period of 8 to 30 days, depending on weather conditions and logistic constraints, the marked plants were again located and removed from below the bird ring for measurement. The terminal ends of a further 20 fresh fronds were removed, measured, weighed, dried and reweighed to obtain length-wet mass and length-dry mass regressions for the apical 3 m of the frond. These regressions were used for growth rate calculations. The conversion of dry mass to carbon was obtained by combusting off the carbon of five finely ground 0.5 g (dry mass) frond sections in a bomb calorimeter. The elemental composition (carbon, hydrogen and nitrogen) of growing tips and the stipe of the frond of material collected during April 1988 was determined using an elemental analyser (CHN - O - Rapid).

Scuba dives were performed to assess holdfast densities in quadrats measuring 4m x 4m and the numbers of fronds per holdfast. For these counts, fronds were separated into canopy (those that reached the surface) and subcanopy categories (those that did not), and counted separately. Some plants were removed entirely for measurements and weighing.

The distribution of the kelp forests was viewed from aerial 1:50000 photographs of Marion Island taken during April 1988. Both Delépine (1976) and Furmanczyk and Zielinski (1982), on the basis of joint aerial photographs and field surveys, demonstrated that macroalgal distributions can be accurately assessed from photographs. Delépine's survey concerned *Macrocystis pyrifera* and *Durvillaea antarctica* at Kerguelen Island. The cover of the algae was determined using an image analyser on these photographs.

Results

Around Marion Island forests of *Macrocystis laevis* are confined almost entirely to the eastern or lee shore (figure 13). The forests reported by De Villiers (1976) on the exposed south-western shore were apparently patchy and were not detectable from the photographs, although three small isolated patches were observed from the aircraft on the exposed shore. Throughout the present surveys the forests rarely extended beyond the 20m isobath, nor shallower than 5m. The total cover of the forest amounted to 5.5 km^2 around the 86 km shore. No photographs of the smaller neighbouring Prince Edward Island are available.

Table 11 summarises the data with respect to holdfast densities, numbers of fronds per plant, frond growth rates and elemental composition. Taking the average holdfast density of 0.87 $plants.m^{-2}$, and an average wet mass per plant of 13.21 kg, the biomass of kelp amounts to 11.55 $kg.m^{-2}$, or 6.34 x 10^7 kg around Marion Island. The conversion of wet mass to carbon is 1 gC = 17.25 g wet mass; the standing stock of kelp thus converts to 3.68 x 10^6 kg carbon. If the amount of kelp around the island is in proportion to its perimeter, Prince Edward Island (with a perimeter of 28km) would support in the region of 2.0 x 10^7 kg wet mass.

Growth measurements have only been possible in the seasons of autumn and late winter. Elongation of the averaged at 4.00 cm during April/May and 6.05 cm per day during August. Growth in the subapical metre measured during April/May 1988 was 26% of the growth in the apical meter. The almost linear length-carbon mass regression for the apical 3m is

$$g\ C = 12.4 \times length(m)^{1.1404},$$

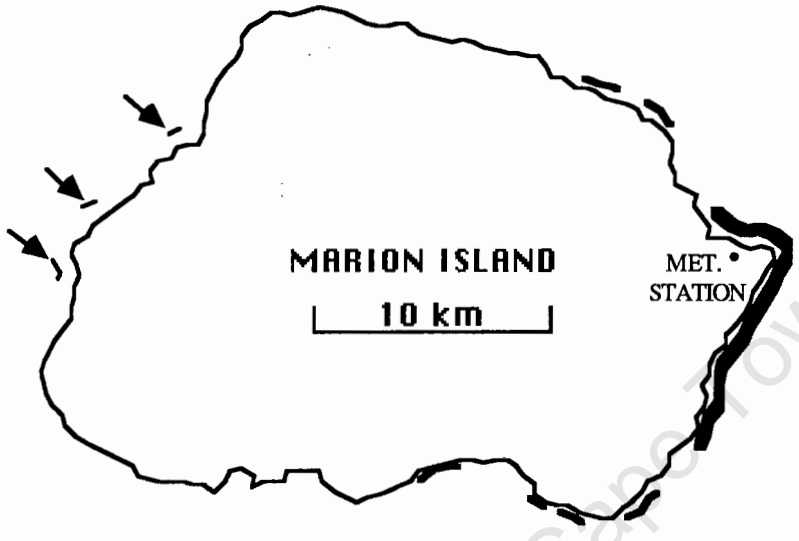

Figure 13: The distribution of Macrocystis laevis around the shore of Marion Island indicated as determined from aerial photography. The bolder line indicates the presence of dense kelp stands, the thin lines on the western shore show the position of sparce stands.

Table 11: Morphometric measurements and carbon, nitrogen and hydrogen content of the kelp *Macrocystis laevis* from the Prince Edward Islands. The quantities of the atomic constituents are expressed as percentage of dry mass. $\bar{x}$ = mean, S.E, = standard error, s = standard deviation, n = sample size.

	$\bar{x}$	S.E.	s	n
Holdfast density (m^{-2})	0.88	0.12	0.32	10 (quadrats)
Fronds per holdfast	14.02	0.95	11.38	142
Plant mass (kg wet mass)	13.21	2.02	6.40	10
Frond growth - APRIL '88				
apical meter ($cm.d^{-1}$)	3.34	0.16	1.25	60
subapical meter ($cm.d^{-1}$)	0.87	0.21	1.23	35
Frond growth - APRIL '89				
apical meter ($cm.d^{-1}$)	2.25	0.29	0.78	7
Frond growth - AUGUST '89				
apical meter ($cm.d^{-1}$)	6.05	0.32	1.59	25
Canopy fronds (% of total)	53	2.85	34	142

	C	H	N
Growing tip	28.21 (±0.25)	4.06 (±0.07)	2.1 (±0.30)
Stipe of frond	29.43 (±1.27)	4.25 (±0.07)	2.9 (±0.14)

which means that fronds produce on average 0.64 gC per day. The number of fronds per holdfast is quite variable, averaging at 14.02 (± 11.0). The average carbon production thus amounts to 7.7 $gC.m^{-2}d^{-1}$ and 11.5 $gC.m^{-2}d^{-1}$ for the months of April and August respectively. A significant difference was apparent between the growth rates during the two seasons in terms of length and mass; greater production being observed during August (T-Test, $P < 0.05$).

The frond length frequency histogram is flat (figure 14). Such a flat distribution suggests that only the largest and oldest fronds are lost by wave action which sets the upper limit of the frond length. The maximum frond length is about 20 m, or twice the depth of the water. Correspondingly the ratio of canopy fronds (those which reach the surface) to subcanopy fronds (those that do not) in water of 10 m depth is 1.1.

Discussion

The southern American populations of *M. pyrifera* occur in far shallower water and over a more restricted range than those off California. Off Puerto Toro, Navarino Island (53°S, 68°W), *M. pyrifera* occurs between the one and nine meter isobaths (Santelices and Ojeda 1984b). Here the shallower limit of its range is set by interspecific competition with the alga *Lessonia vadosa*, and the deeper limit by a lack of hard substratum for attachment. Where consolidated rock did extend to 15 m, a dense stand of *L. flavicans* bordered the seaward extent of *M. pyrifera*. Light limitation is believed to restrict the competitive ability of *M. pyrifera* at its seaward extent, while tolerance to wave action is the factor operating at the shallow extent. Other sites in this vicinity show the same algal zonation, but there is great variation on the upper and lower extent of *M. pyrifera*.

The shallow subtidal zone at the Prince Edward Islands has a similarly well defined zonation of foliate macroalgae; at the low water mark the dominant species is *Durvillaea antarctica*, whereas at successively greater subtidal depths *D. willana, Desmarestia rossii* and *M. laevis* dominate (Beckley and Branch, in prep.). De Villiers' (1976) account of *M. laevis* on the exposed shore of Marion Island indicated that beds were patchy there and restricted to deep water. The lee shore of Marion Island is subjected to more moderate wave exposure.

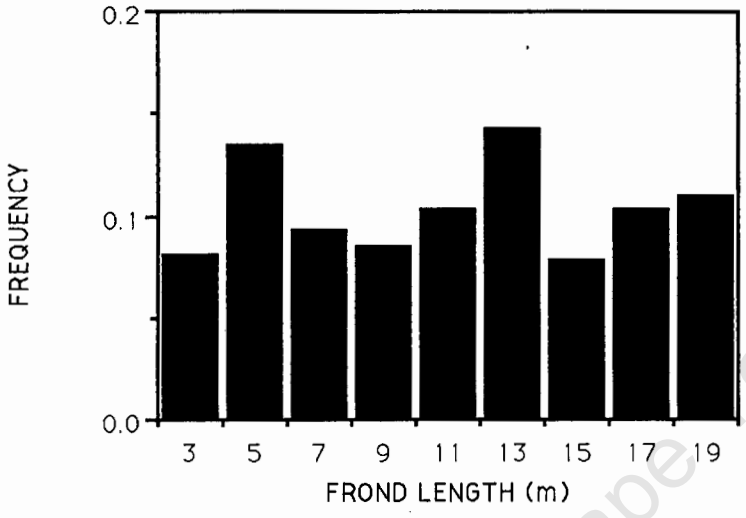

Figure 14: The frequency distribution of Macrocystis laevis frond-lengths (in categories of 2 m intervals), from a sample of five plants.

Nevertheless, the estimates presented below indicate that frond loss may be substantial even in the lee of the island.

Over one period of 30 days no less than 85% of the marked fronds disappeared, and over shorter periods of less than 10 days at least 30% of the marked fronds were lost. The observations were too few to derive a reliable estimate of the rate of frond loss. In addition, these observations apply only to the rate of loss of mature canopy-forming fronds, and will therefore over-estimatie the average frond loss. It is, however, possible to estimate the average rate of frond loss from the rate of frond initiation assuming that the number of fronds remain constant (which is not necessarily the case). With a flat frond-length frequency distribution, a growth rate of 4.09 cm per day, and 14 fronds per holdfast reaching a maximum length of 20 m, a loss of one frond per holdfast every 35 days would be expected if the plant mass is to remain unchanged.

The mean biomass of *M. laevis*, 11.55 $kg.m^{-2}$ (wet mass), is similar to that of *M. pyrifera* at Kerguelen Island, for which Delépine (1976) reports a range of 3.4 - 22.5 $kg.m^{-2}$ and a mean between 7 and 12 $kg.m^{-2}$ for kelp within the 20 m isobath. The maximum macroalgal biomass at Borge Bay, South Orkney Islands, including the genera *Desmarestia* and *Himantothallus*, measured was only 2.05 $kg.m^{-2}$ (Richardson 1979). This low maximum Richardson attributes to ice-scouring and ice-shading during winter.

Both the biomass and production of *M. laevis* can be expected to increase during the long summer days. Frond growth rates during August were greater than during April; this Van Tussenbroek (1989) found to be the case for the fronds of *M. pyrifera* at the Falkland Islands also. While increased light availability increases the growth rate, a biomass change is most likely to be caused by a change in the rate of frond initiation or of loss. A greater number of fronds per holdfast is expected during summer (Jackson 1987). Increased water turbulence in winter would also result in a decrease in the size of the largest frond and hence the number of fronds on the holdfast.

The production rate of between 7 and 11 $gC.m^{-2}.d^{-1}$ must be considered as net production. The simple method employed here, ie. measuring length increments, contrasts with assessments of carbon fixation by ^{14}C incubations or by changes in O_2 concentrations.

These latter techniques have yielded gross production values for *M. pyrifera* off California ranging from 6.8 to 12 $gC.m^{-2}.d^{-1}$ (Towle and Pearse 1973, McFarland and Prescott 1959). Besides these, I could find no direct measurements of net production with which to compare the growth of *M. laevis*. No growth measurements of *M. laevis* have yet been made during summer and, until such time, the estimate of yearly production based on the winter values reported here, ±3500 $gC.m^{-2}.y^{-1}$, should be regarded as an underestimate.

Table 12 compares the daily input of organic matter in the Prince Edward Island Seas from various sources. Although more productive than phytoplankton per unit area, the macroalgae contribute the least to the organic input to the seas around the islands as they occupy only a small fraction of the area inside the 500m isobath. *M. pyrifera* does not loose excessive amounts of carbon via abrasion with rock surfaces. While *M. laevis* does not abrade, the loss of basal blades on the stipe is evident. Exudation of dissolved organic carbon from *M. integrifolia* is less than 5% of production (Fankboner and deBurgh 1977) and there is no reason to assume that it will be much different for *M. laevis*. Only two types of grazers are found in reasonably high numbers in the kelp forests of *M. laevis*, these being the sea urchin *Pseudechinus marionus* (up to 50 m^{-2} or 67 $g.m^{-2}$ wet mass) and several isopods dominated by *Dynamenella eatoni* (up to 4197 m^{-2} or 42 $g.m^{-2}$ wet mass) (Beckley and Branch, in prep.). The diet of these grazers is unknown, though they may not be grazing live material (they were not observed on live plants), but rather dead fronds as is the case in several south American communities (Castilla and Moreno 1982, Dayton 1985). In the absence of direct herbivory it would appear that the fate of the kelp is either to deposit on the shore where it fuels a decomposer community (Crafford and Scholtz 1987), or to wash to sea. Crafford (1984) however notes that while decomposing *D. antarctica* fronds are heavily colonised by endemic dipteran larvae, the fronds of *M. laevis* are avoided by macrofauna. The benthic community of the South Orkney Islands displays a similar paucity of direct herbivory and a preponderance of detritivores (Richardson 1979). Although the presence of productive *M. laevis* forests may have a pronounced influence on the benthic community structure around the islands, the contribution of this kelp's production to the ecology of the island seas would seem to be limited.

Table 12: A comparison of the various sources of organic carbon input into the Prince Edward Island Sea, as estimated in the month indicated. The phytoplankton production estimate is the mean of a highly variable data set.

Source	$gC.m^{-2}.d^{-1}$	Month	Reference
Durvillaea antarctica	7.1	Year round	Haxon and Grindley 1983
M. laevis	7.7	April	This study
M. laevis	11.5	August	This study
Phytoplankton	2.1	April	Duncombe Rae 1988
Introduced material	4.63	April	Perissinotto 1989

References

Adams, N. J. (1990) Feeding biology and ecology of King *Apterodytes patagonicus* and Gentoo *Pygoscelis papua* at marion island. Unpublished PhD thesis, University of Cape Town, Cape Town, South Africa.

Boden, B. P. (1988) Observations of the Island mass effect in the Prince Edward Archipelago. *Polar Biol.*, 9, 61-68.

Castilla, J. C. (1985) Food webs and functional aspects of *Macrocystis pyrifera* kelp community in the Beagle Channel, Chile. In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried , P.R. Condy and R.M. Laws, editors, Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, p.407-414.

Castilla, J. C. and C. Moreno (1982) Sea urchins and *Macrocystis pyrifera*: Experimental tests of their ecological relations in southern Chile. In: *International Echinoderm conference,* J. M. Lawrence, editor, Tampa Bay, AA Balkema, Rotterdam pp. 257 - 263.

Chapman, A. R. O. (1981) Stability of sea urchin dominated barren ground following destructive grazing of kelp in St. Margaret's Bay, Eastern Canada. *Mar. Biol.*, 62,307 - 311.

Crafford, J. E. (1984) Life cycle and kelp consumption of *Paractora dreuxi mirabilis* (Diptera; Helcomyzidae): a primary decomposer of stranded kelp at Marion Island. *S. Afr. J Antarct. Res.*, 16, 42-84

Crafford, J. E. and C.H. Scholtz (1987) Phenology of stranded kelp degradation by the kelp fly *Paractora dreuxi mirabilis* (Helcomyzodae) at Marion Island. *Polar Biol.*, 7, 289-294.

Dayton, P. K. (1985) The structure and regulation of some south American kelp communities. *Ecol. Monogr.*, 55(4), 447-468.

De Villiers, A. F. (1976) Littoral ecology of Marion and Prince Edward Islands (Southern Ocean). *S. Afr. J. Antarct. Res..*, Suppl 1, 1-40.

Delépine, R. (1976) Note preliminaire sur la repartition des algues marines aux Iles Kerguelen. *C.N.F.R.A.* , 39, 153 - 159.

Duncombe Rae, C. M. (1988) Data report of the first cruise of the Marion off-shore ecological study (MOES-I). *S. Afr. Nat. Prog. Rep.*, 159, 384 pp.

El-Sayed, S. Z., P. Benon , P. David, J. R. Gridley and J.- F. Murial (1979) Some aspects of the biology of the water column studied during the 'Marion Dufresne' cruise 08. *C. N. F. R. A.*, 44, 127-134.

Fankboner, P. V. and M. E. De Burgh (1977) Diurnal exudation of ^{14}C-labelled compounds by the large kelp *Macrocystis integrifolia* Bory. *J. exp. mar. Biol. Ecol.*, 28, 151-162.

Furmanczyk, K. and K. Zielinski (1982) Distribution of macroalgae groupings in shallow waters of Admiralty Bay (King George Island, South Shetland Islands, Antarctic), plotted with the help of air photograph analysis. *Pol. Polar Res.*, 3(1-2), 41-47.

Hay, C. H. (1986) A new species of *Macrocystis* C. Ag. (Phaeophyta) from Marion Island, southern Indian Ocean. *Phycologia,* 25, 241-252.

Haxen, P. G. and J. R. Grindley (1985) *Durvillea Antarctica* production in relation to nutrient cycling at Marion Island. In: *Antarctic nutrient cycles and food webs,* W. R. Siegfried, P. R. Condy and R. M. Laws, editors, Springer-Verlag, Berlin, Heidelberg, New York, Tokyo, 637 - 640.

Jackson, G. A. (1987) Modelling the growth and harvest yield of the giant kelp *Macrocystis pyrifera. Mar. Biol.*, 95, 611-624.

Leighton, D. L., L. G. Jones and W. J. North (1966) Ecological relationships between giant kelp and sea urchins in southern California. *Proceedings of the International Seaweed symposium*, 5, 141-153.

Mann, K. H. (1973) *Ecology of coastal waters. A systems approach.* Blackwell Scientific Publications, Oxford, London.

McFarland, W. M. and J. Prescott (1959) Standing crop, chlorophyll content and in situ metabolism of a giant kelp community in southern California. *Publ. Inst. Mar. Sci. Univ. Texas*, 6, 215-240.

Perissinotto, R. (1989) The structure and diurnal variations of the zooplankton of the Prince Edward Islands: implications for the biomass build-up of higher trophic levels. *Polar Biol.*,9, 505-510.

Perissinotto, R., C. M. Duncombe Rae, B. P. Boden and B. R. Allanson (1990) Vertical stability as a controlling factor of the marine phytoplankton production at the Prince Edward Archipelago. *Mar. Ecol. Prog. Ser.*, 60(1/2), 205-209.

Richardson, M. G. (1979) The distribution of Antarctic marine macro-algae related to depth and substrate. *Br. Antarct. Surv. Bull.*, 49, 1-13.

Santelices, B. and F. P. Ojeda (1984a) Population dynamics of coastal forests of *Macrocystis pyrifera* in Puerto Toro, Isla Navarino, southern Chile. *Mar. Ecol. Prog. Ser.*, 14, 175-183.

Santelices, B. and F. P. Ojeda (1984b) Effects of canopy removal on the understory algal community structure of coastal forests of *Macrocystis pyrifera* from southern south America. *Mar. Ecol. Prog. Ser.*, 14, 165-173.

Skottsberg, C. (1921) Botanische Ergbnisse der Schwedischen Expedition nach Patagonien und dem Feuerlande 1907-1907, *K. Sv. Vetensk. Akad. Handl.*, 61, 1 - 56 .

Towle, D. W. and J. S. Pearse (1973) Production of the giant kelp, *Macrocystis*, by in situ incorporation of ^{14}C in polyethylene bags. *Limnol. Oceanogr.*, 18, 155-159.

Van Tussenbroek, B. I. (1989) Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falkland Islands. *Mar. Biol.*, 100, 419-430.

Chapter 4

Patterns in the benthic communities on the shelf of the Prince Edward Islands

Abstract-Benthic communities at the Prince Edward Islands were sampled qualitatively with an epi-benthic sled at 57 stations over a five year period. Additional impressions of these communities were obtained from replicate underwater photographs. The sled was found to be an ineffective sampler on rocky substrata, while the presence of several major taxa was missed on the photographs although they were found in sled samples. Macrofaunal species diversity was impoverished compared to Antarctic communities. This is ascribed to the extreme isolation and geological youth of the islands. A cluster-analysis based on species abundance alone aggregated most stations into 8 recognisable communities. Each of these communities had a unique depth and substratum combination. Indicator species are listed for each of the groups. Deep, rocky substrata were dominated by Porifera, bryozoans and cnidarians, while soft-substrata were dominated by polychaetes, bivalves and brachiopods. Errant forms consisted predominantly of echinoderms, with crustaceans being important in shallower habitats. Filter feeders dominated the islands' benthos. The shrimp *Nauticaris marionis* was abundant everywhere. The likely influence of the islands' oceanographic processes on the benthos is discussed, including the repeated massive diatom blooms which are a frequent occurrence, and the possibility of current eddies.

Introduction

The Prince Edward Islands of the sub-Antarctic Indian ocean are among the most isolated of terrestrial and shallow marine environments around the globe. Situated at 46°50'S; 37°50'E, they lie 2300 km from the nearest continental land mass, and 760 km from Crozet Island. The islands are also relatively young, their volcanic origen being dated at approximately 276000 years before present (McDougall 1971). The volcano on which the islands rest elevates about 1000 km^2 of ocean floor to within 200 m of the ocean surface. Despite the intrinsic interest of the islands, collections of the benthic fauna have been limited. Prior to this survey marine benthic invertebrates were collected on the voyage of the Challenger in 1873, by the French Bouganville Expedition in 1939, by the South African Biological and Geological Expedition in 1965-1966 and by the French expedition of the 'Marion Dufresne', 1976. A systematic account of the South African collections was published by Van Zinderen Bakker et al. (1971), based on the benthic sampling in intertidal habitats, by divers or among material cast ashore. De Villiers (1976) conducted a thorough study of the fauna and flora of the intertidal community, and provided descriptions of these communities. The present report is based on an extensive survey of the benthic fauna of the Prince Edward Islands, which was conducted on 8 relief voyages of the 'M.V. S.A. Agulhas' between 1984 and 1989. Specimens were collected from depths ranging from 30 to 880 m at 57 sites around the islands.

Being isolated and geologically young, the islands' terrestrial communities are not diverse and have few endemic species (Van Zinderen Bakker et al. 1971). Although the easterly flow of the Antarctic Circumpolar Current provides a route for colonisation for marine species from similar latitudes in the west, about 50% of the Antarctic benthic invertebrates apparently do not have pelagic larval life stages (Thorson 1950, White 1984). As a result, endemism in the Antarctic is high and colonisation slow. The Prince Edward Islands are thus not likely to have as diverse a benthic community as that of the older Kerguelen and Crozet Islands or the South American continental shelf.

One of the major points of interest to biologists working on the communities of this island group are the sources of production which sustain large stocks of marine mammals and birds resident on the island. The problem is interesting as the sub-Antarctic ocean is characterised by

very low primary production. The archipelago itself provides an 'island-mass effect' which results in high production by planktonic diatoms locally, although the transfer of this energy to zooplankton is very inefficient (Perissinotto, in press). The benthic community is now believed to play an important role in sustaining the avifauna (Perissinotto and McQuaid 1990). The trophic dynamics of these benthic communities is still unknown. Furthermore, no quantitative estimates of benthos have yet been obtained, partly because of the difficulty and expense of doing so at these remote islands. This paper is a report on the classification of the benthic communities based on the extensive qualitative sampling program recently completed. It is intended to form a foundation for understanding the structure of the benthos and its trophic role in the food-webs of the arcgipelago.

Physical environment

Figure 15 shows the bathymetry of the region. The older, exposed grey lavas have been dated to 276000 (± 30000) years before present. The last volcanic activity occurred about 15000 (± 8000) years before present resulting in black lava (McDougall 1971).

Sea-surface temperatures fluctuate between 4° and 8°C, variations depending largely on the position of the weak sub-Antarctic front (SAF). This poorly-understood front lies on average just north of the islands, but meanders considerably (Lutjeharms and Valentine 1984), sometimes moving across the isands. Mean mid-summer and mid-winter sea-surface temperatures differ by only 1.5°C. Vertical temperature profiles show the existence of a highly variable, often tenuous thermocline. Typically the temperature at 50 m depth is the same as that of the surface, whereas at 200 m, 500 m and 1000 m the temperatures are 3 - 5°C, 2.5 - 3.5°C and 2.6°C respectively.

Methods

The benthic communities on the Prince Edward Islands were sampled at 57 stations (figure 15) over a range of depths from 30 to 880 m with an epi-benthic sled (figure 16). At each station the sled was dragged from the stern of the 'M.V. S.A. Agulhas' at a maximum velocity of 2 knots for approximately 10 minutes. The entire sample was sieved through a 12 mm and a 1

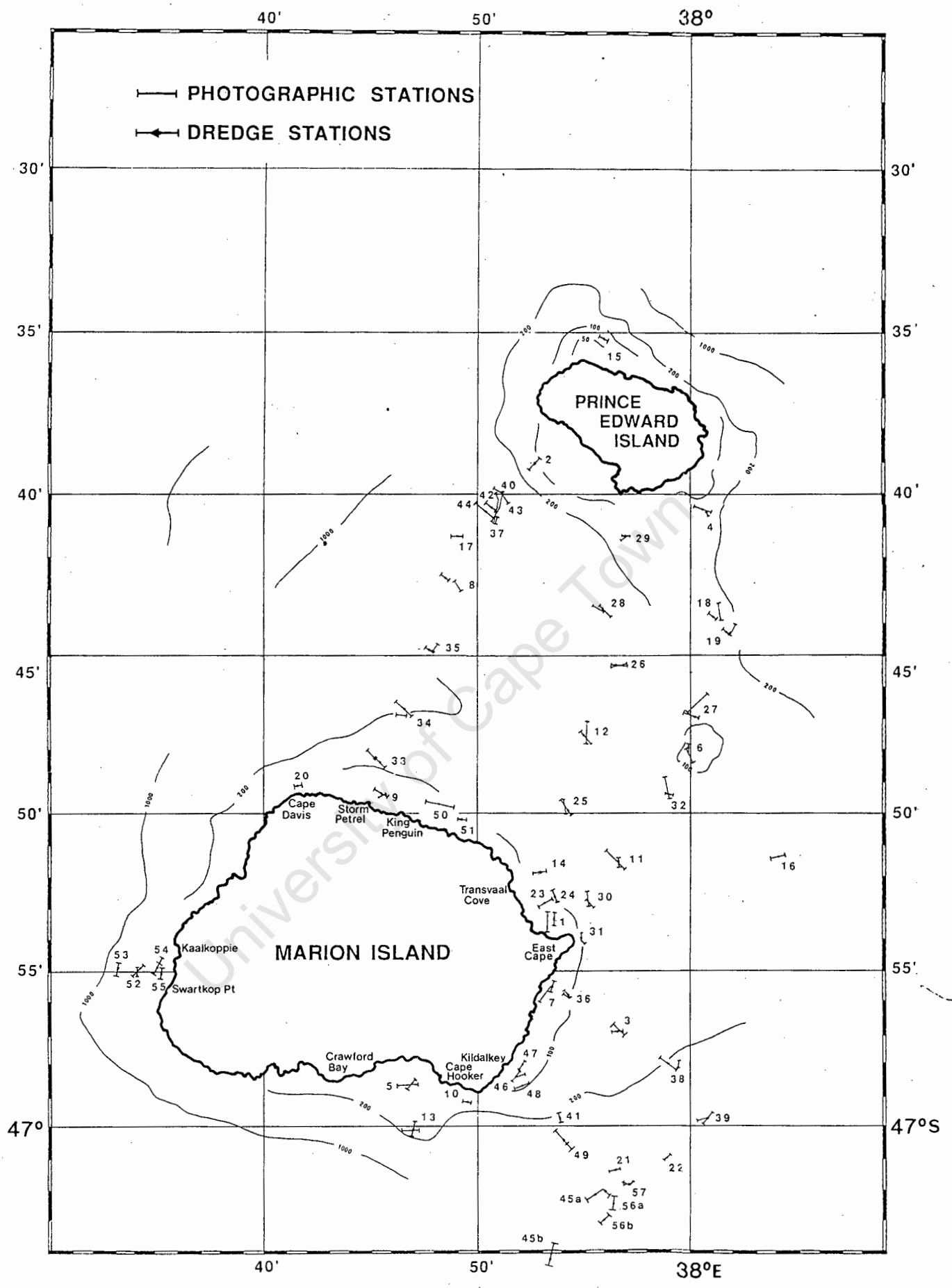

Figure 15: A map of Marion and Prince Edward Island on which are plotted the positions of the 57 stations at which the benthic fauna was sampled.

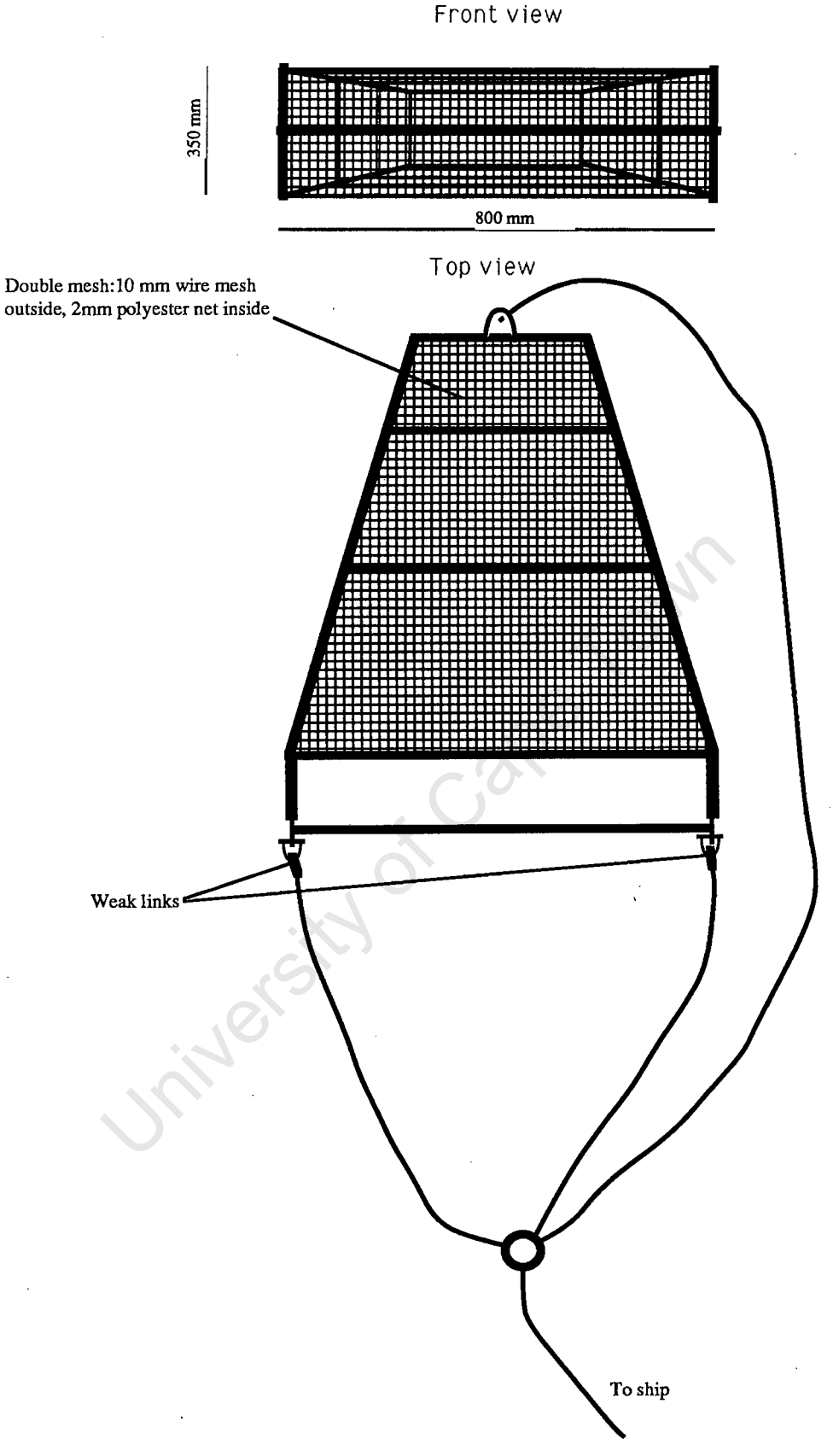

Figure 16: The epi-benthic sled used in this survey.

mm sorting tray. In cases where an excessive amount of material filled the sled, a sub-sample of 100 l volume was sorted, while the remainder was searched superficially for rare specimens in case they were not represented in the sub-sample. Sediment samples collected by the sled were retained for a geological classification upon return to Cape Town. All retained specimens were sorted by species and fixed in a 4% formalin solution. In Cape Town the specimens were identified and counted. Identification was based on a series of keys to the fauna developed by Branch et al. (in prep.).

Soft-sediment samples were split into the three components: gravel, sand, mud (silt and clay) and the proportion of each was quantified. The gravel fraction was separated by dry-sieving the entire sample through a 2 mm sieve. The remainder was sieved under water through a 63 µm sieve to retain the sand fraction, the fraction which passed through being classified as silt and clay, collectively termed mud. On the basis of these proportions, and the occurrence of rock estimated from photographs, substrata were classified into 6 types (the codes which appears in parentheses are used in table 13); viz. (0) > 50 % rock, (1) 10 - 50 % rock, (2) > 20 % gravel, (3), 5 - 20 % gravel, (4) >5 % mud and (5) > 95 % sand.

A series of underwater photographs (up to 60) were taken at most stations. A wide-angle camera was mounted in a pressure housing on either side of which was mounted a flash. The camera was lowered until it was 2 m from the bottom, at which point a rod, suspended from the chamber, triggered the camera and the flashes as it made contact with the sea-bed. The chamber was raised and re-lowered to 2 m from the bottom after each photograph to reposition the camera and to recharge the battery. The area of sea-bed pictured in each photograph was 1.0 m^2. Not all photographs were successful, for many were out of focus or the flash failed to operate. Up to 12 of the clearest photographs were used for counting specimens and for assessing the area covered by organisms.

Statistical methods

Species abundances were transformed into ranks according to the following rules:

rank 0	absent
rank 1	1 - 5 animals

rank 2	6 - 15 animals
rank 3	16 - 30 animals
rank 4	31 - 50 animals
rank 5	51 - 100 animals
rank 6	101 - 300 animals
rank 7	301- 1000 animals
rank 8	> 1000 animals

Sponges and bryozoans, which could not be counted as individuals, were catagorised by volume:

rank 0	absent
rank 1	< 5ml
rank 2	5 - 25 ml
rank 3	25 - 75 ml
rank 4	75 - 250 ml
rank 5	250 - 500 ml
rank 6	500 - 1500 ml
rank 7	1500 - 3000 ml
rank 8	> 3000 ml

Samples (or stations) were clustered by the Bray-Curtis similarity index based on species abundance expressed by rank. A dendrogram was created by the group-average sorting procedure, which joins two groups of samples at their average level of similarity. Abundant species were not downweighted. The percentage contribution of each species towards the average Bray-Curtis dissimilarity between two groups was used to extract the important diagnostic species of each group. A further criterion for selecting indicator species was that they be present in all the stations of one cluster, but absent (or very rare) in all the stations of the sister cluster. Differences in depths and the frequency of substratum types between groups were tested using one-way ANOVA and two-way CHI-Square tests respectively.

Differences between the chance of a taxon being recorded as present by the sled technique and by the photographic technique were tested with a one-sample t-test. A taxon was assigned the value 1 for a particular station and if it was recorded as present. The difference between the presence/absence score of the sled technique and of the photographic technique was computed for each major taxon for each station. This value was either -1 (recorded by photographs but

not found in the sled sample), 0 (recorded as present or absent alike by both techniques) or 1 (found in the sled sample but not in the photographs). If the 95% confidence interval of the mean difference between the presence (1) or absence (0) score for all stations did not include zero, the null hypothesis (that both techniques record taxa equally well) was rejected.

Results

Table 13 lists the (1) number of species recorded, (2) the depth, (3) the substratum type, (4) the percentage of ground covered by animals, and (5) the proportion of species of each feeding type for each of the 57 stations sampled. In total 546 nominal species were recorded, 41% of which were new records for the islands, and about 10 % of which were undescribed. Between 0 and 70 species were recorded at each station. The number of species recorded per station was not related to depth nor the substratum type. The percentage of ground covered by living organisms was 32.5% on average for all stations, but was extremely variable (s = 24.8%). Of this variation, 21.5% was explained by a negative exponential correlation with depth ($p < 0.01$); the deep stations had much less ground covered than shallow stations. There was, however, no difference in percentage ground cover between substratum types.

Figure 17 shows the distribution of various substratum types around the two islands. The substratum has been sampled only at the 57 stations which formed part of this work. Generally the central plateau and inshore stations in the lee of the two islands are characterised by soft-substrata, whereas rocky-substrata form the deeper and sloping ground on the edge of the plateau and on the inshore, exposed coasts. A one-way ANOVA shows considerable overlap in the depth ranges of the substratum types, but also that the stations with rocky-substrata occur at greater depth than stations with soft substrata. The soft-sediment samples were similar throughout, being composed of sand (90.7 %, sd = 15.4 %), gravel (5.2 %, sd = 14.9 %), clay (0.9 %. sd = 1.3 %) and silt (2.3 %, sd = 4.3 %). The gravel component was most variable, influenced by only a few stations predominated by gravel. The efficacy of the dredging technique and of the photographic technique for recording specimens from the respective phyla were compared from presence/absence information. The null hypothesis, that the probability of a

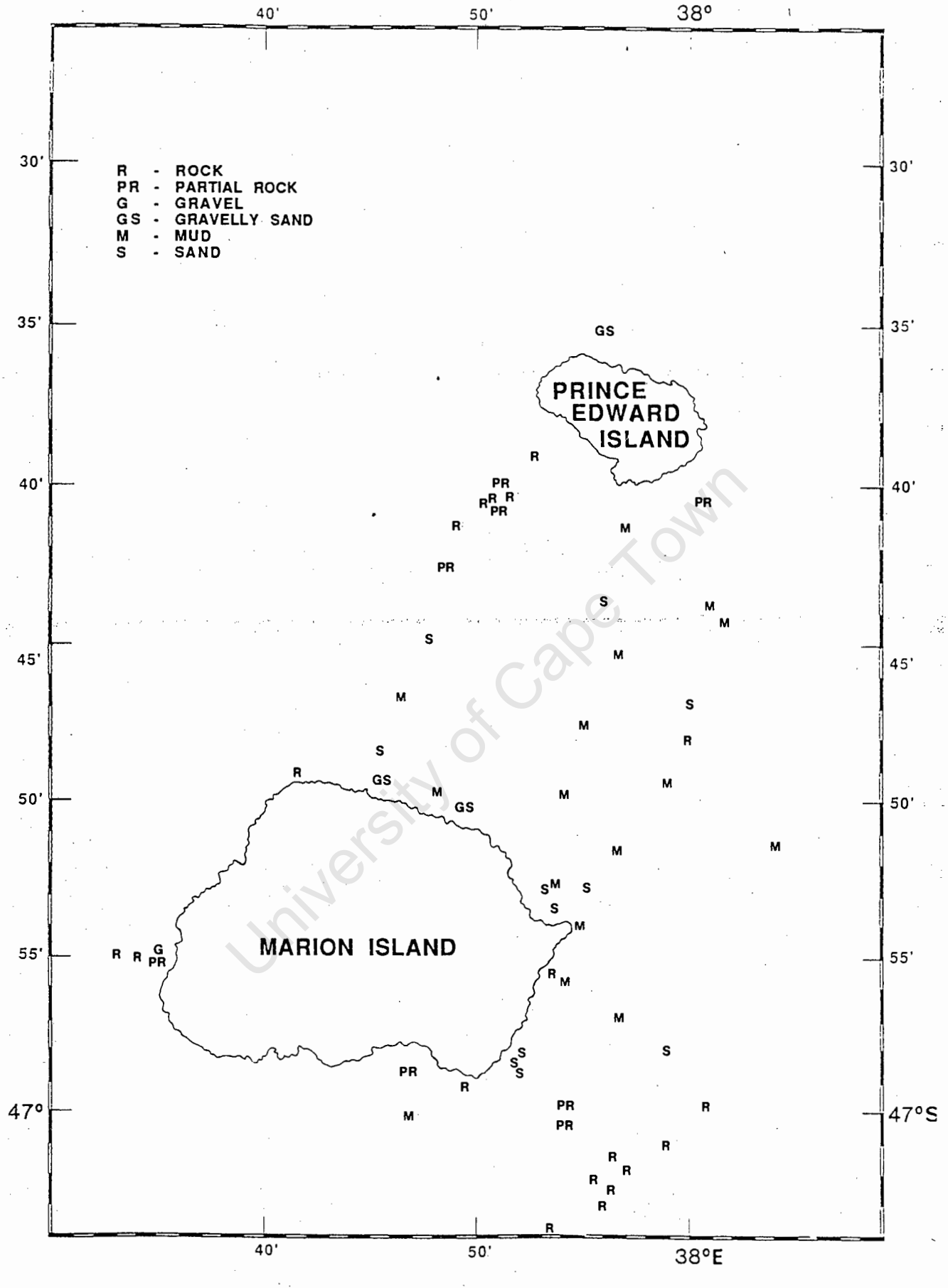

Figure 17: The substratum types as determined from photographs and from samples retrieved from the sled.

TABLE 13: A listing of the some physical and biological information of each station sampled. The code for substratum type is explained in the text (see p 77).

Station	Depth (m)	Substratum	# species	% cover	% Filter feeders	%Deposit feeders	% Grazers	% Predator Scavengers
1	90	5	46		51	40	0	8
2	125	0	38		55	36	3	6
3	135	4	38	38.2	59	34	0	7
4	147	1	28	41.1	47	49	0	4
5	71	1	16	15.3	62	38	0	0
6	52	0	38	76.8	56	36	0	8
7	44	0	16	56.6	70	27	0	3
8	255	1	34	14.1	58	32	0	9
9	44	3	15	1.3	41	55	0	3
10	72	0	8		50	50	0	0
11	132	4	43	29.5	66	24	1	8
12	151	4	58	34.7	59	23	1	17
13	140	4	65	14.3	57	26	1	17
14	85		40	56		35	0	9
15	49	3	46		33	45	1	21
16	165	4	56		64	23	1	12
17	355	0	54		54	21	3	22
18	228	4	49	8.6	61	29	0	10
19	210	4	42	22.8	58	30	2	9
20	38	0	35		29	48	6	17
21	350	0	9		50	22	0	28
22	391	0	31		74	13	0	13
23	31	5	15	69.2	63	25	4	8
24	107	4	39	35.1	55	33	2	11
25	139	4	68	37.0	69	18	2	10
26	179	4	57	7.9	72	23	1	4
27	112	5	46	79.8	79	14	0	7
28	240	5	58		69	22	1	8
29	145	4	43	51.9	77	20	0	3
30	120	5	48	64.7	68	21	3	8
31	63	4	43	59.6	58	29	0	13
32	147	4	43	38.9	77	21	0	3
33	110	5	40	44.0	67	25	0	8
34	208	4	34	13.2	83	13	0	5
35	204	5	29	7.0	59	28	1	12
36	106	4	45	98.8	76	18	0	6
37	474	1	64	18.8	64	23	1	13
38	200	5	61	30.6	77	16	0	6
39	368	0	68	2.3	66	19	3	12
40	420	5	34		44	37	4	15
41	210	0	44		69	15	0	16
42	510	0	70	20.6	68	17	0	14
43	475	0	58	25.8	58	25	1	15
44	527	0	65		56	27	0	17
45	480	0	29		88	9	0	3
46	49	5	12	18.5	37	42	5	16
47	52	5	39		61	23	2	13
48	98	5	43		54	29	0	17
49	290	1	47	7.5	73	16	0	11
50	45	4	0					
51	50	3	28		55	26	2	17
52	370	0	28	7.2	59	22	0	20
53	693	0	31		59	22	0	20
54	102	2	52	42.2	63	23	1	13
55	45	1	43		44	27	7	21
56	750	0	8.0		38	31	0	31
57	697	0	253	0.3	63	4	4	29

phylum/class being recorded as present is the same for both techniques, was rejected for bryozoans, hydrozoans, polychaetes and ophiuroids, which had a greater chance of being represented in a sled sample than from being detected in a photograph. Fish and octocorals were recorded best by photographs, although it is possible that many hydrozoans were mistakenly identified in the photographs as octocorals. As the abundance scores were estimated from several photographs (5 - 12) it was possible to estimate the distribution pattern from the ratio of the variance (s^2) to the mean (Zar 1984). If the ratio exceeded 1.0 ($p < 0.05$, t-test) the distribution was assumed to be clumped, whereas if the ratio was not different from 1.0 the distribution was assumed to be random, or regular if less than 1.0. Again, data were lumped by phylum or class, the effect of which was to reduce the likelihood of diagnosing a non-random distribution, where individual species might have been non-randomly distributed. Hydrozoans, anthozoans, bivalves, echinoids, asteroids and gastropods appeared irregularly in replicate photographs from each station.

The majority of animals dredged per station, 60.3% (s = 12.2%), were filter feeders, 22.5% (s = 10.8%) were deposit feeders, and 11.9% (s = 7.5%) were predators/scavengers. No trend or differences in these proportions were evident with respect to depth or substratum type.

Figure 18 is a dendrogram of samples based on the Bray-Curtis similarity index. The variability in species scores was high (CV ranges from 1 to 3) and the similarity between samples was low in general, no stations being more than 70% similar. Figure 19 maps the groups of samples which are at least 40% similar on average. Eight clusters occur, which form recognisable communities each with unique depth and substratum combinations. Eleven stations were regarded as outliers; they showed less than 40% similarity with any other station. An analysis of variance confirms that the depths of these eight groups are significantly different ($p < 0.05$). The relative frequency of occurrence of each substratum type in each group was tested with a two-way Chi-Square test, which showed that the proportion of substratum types in each group were also different ($p < 0.05$). Those communities in depths > 100 m were less

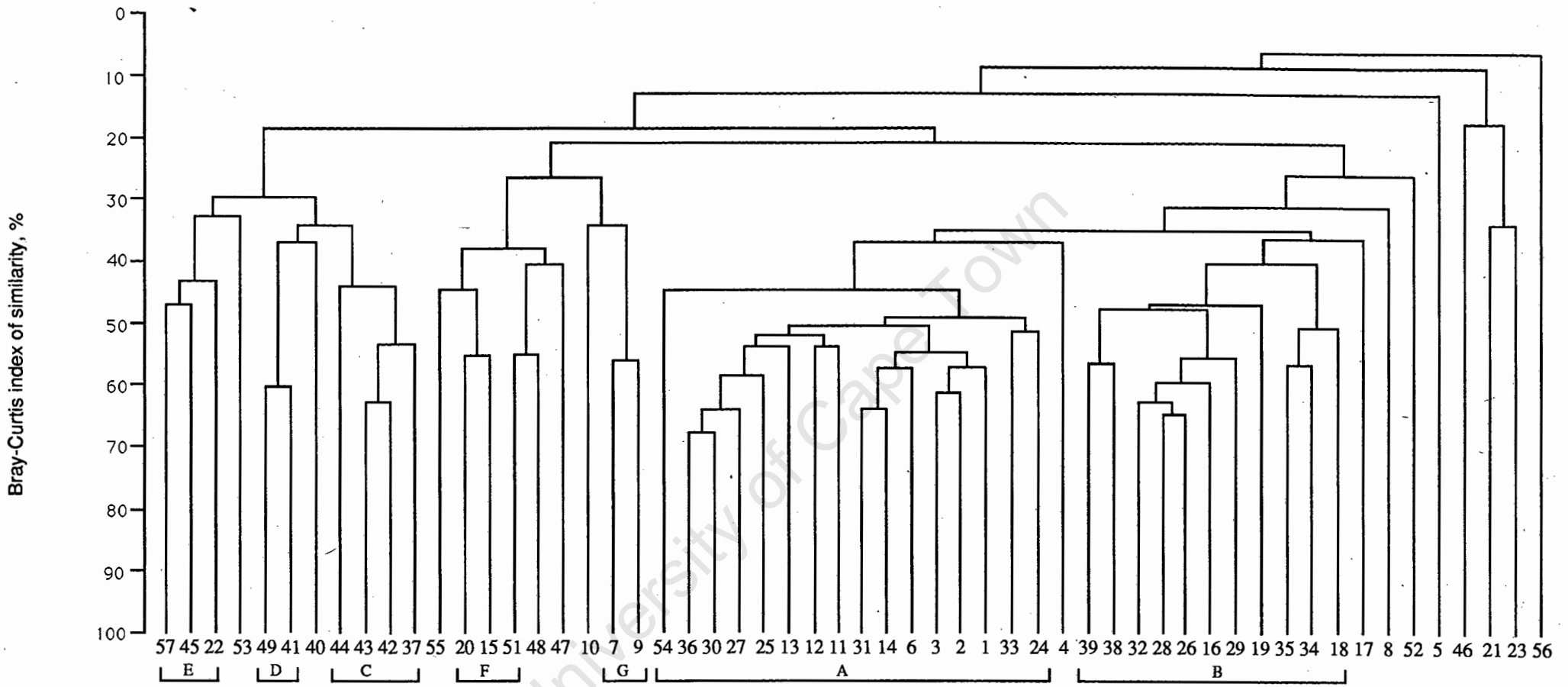

Figure 18: A dendrogram of stations based on ranked species abundance. The eight groups discussed in the text (lettered A to H, p. 81) are indicated here.

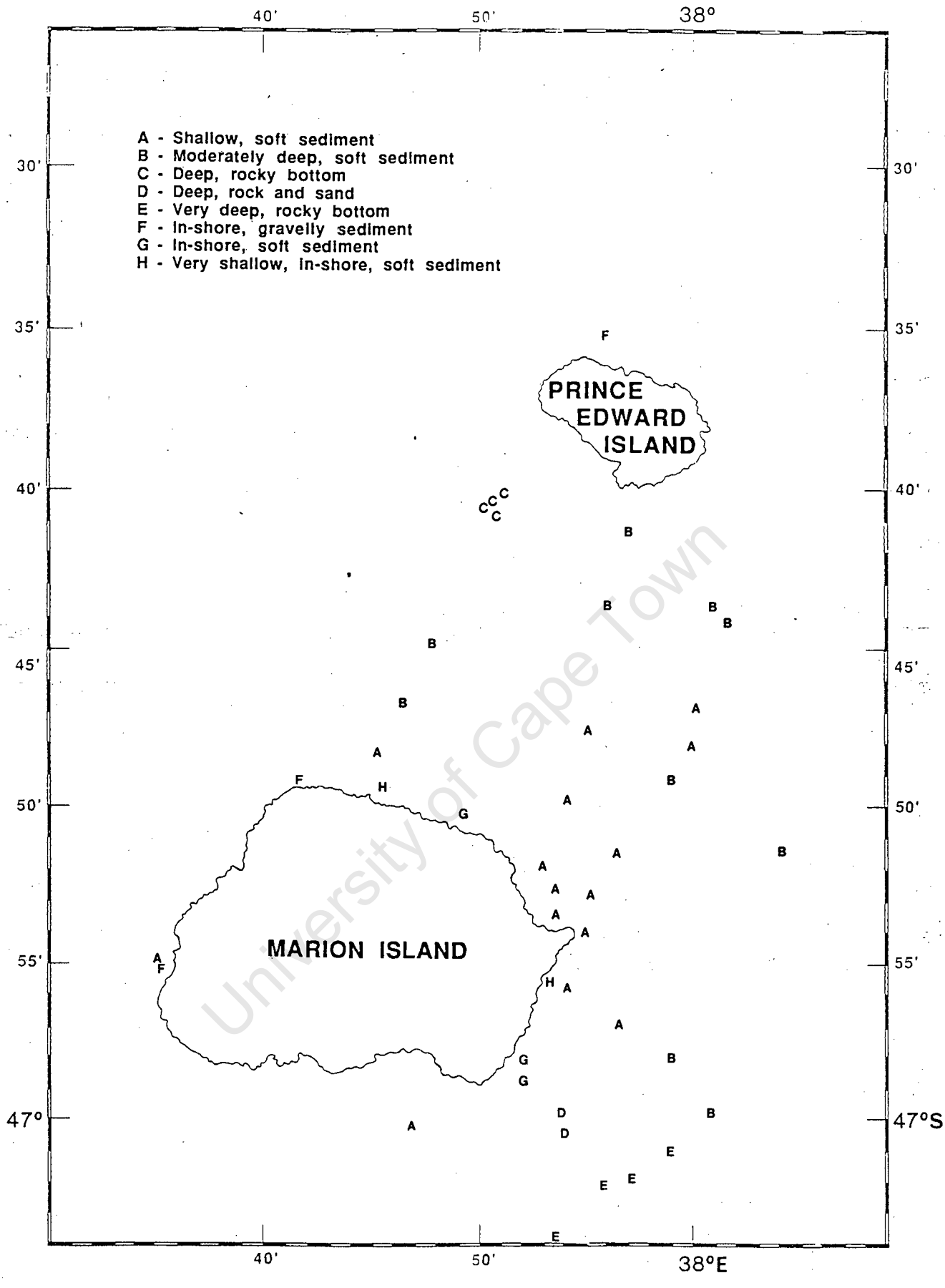

Figure 19: A map showing those station which are at least 40% similar with respect to their ranked species abundances.

variable than those close inshore. Samples taken immediately adjacent to the islands tended to be unique, most not clustering with any other station.

The important diagnostic species and the physical characteristics of the groups, are displayed on a dendrogram, simplified to show only the dichotomies of major groups (figure 20). The diagnostic species are not necessarily the most abundant in a group, but rather those which distinguish one group from another. Several more species presented themselves as candidate indicators than are represented. The selection, although not entirely objective, favoured non-colonial, easily identified species which contributed substantially to the average dissimilarity between the groups. The physical characteristics of the major groups and the species constituting at least 50% of the animals in a group are listed below (groups are displayed figures 18 and 19).

Soft sediment, moderate depth: Group A was the largest group, with 16 stations (at 43% similarity). This group of stations dominated the moderately shallow (45 - 150 m) section of the inter-island plateau, predominantly in the lee of Marion Island extending to the Natal Bank. In all except one of these stations (station 2) the substatum was characteristically soft-sediment. *Pseudechinus marionis* (Echinoidea), *Nauticaris marionis* (Decapoda), *Ophiurolepas intorta* (Ophiuroidea), *Tervia irregularis* (Bryozoa), *Lanice conchilega* (Polychaeta) and *Limatula pygmaea* (Bivalvia) accounted for > 50% of the animals recorded in these stations.

Eleven stations clustered at 40% similarity to form group B and were distributed in deeper water surrounding the previous group. The depth of these stations ranged between 145 and 370 m, and all had soft-sediment. *Ophiocten amitinum* (Ophiuroidea), sponges, *Lanice conchilega* (Polychaeta), *Diatosula marionensis* (Bryozoa), *Pseudechinus marionis* (Echinoidea) and *Magellania kerguelenensis* (Brachiopoda) accounted for > 50% of the animals recorded in this group.

Rocky bottom, deep water: Three groups of samples were associated with deep (> 300 m), rocky substrata. Four stations south-west of Prince Edward Island emerged as a unit at 43% similarity (group C). They occurred at depths of between 470 and 530 m, all with rocky substrata. Sponges, *Thourella variabilis* (Octocarallia), *Ogivalia elegans* (Bryozoa), *Arcturides cornutus* (Isopoda) and an unidentified crinoid species accounted for > 50% of the animals in

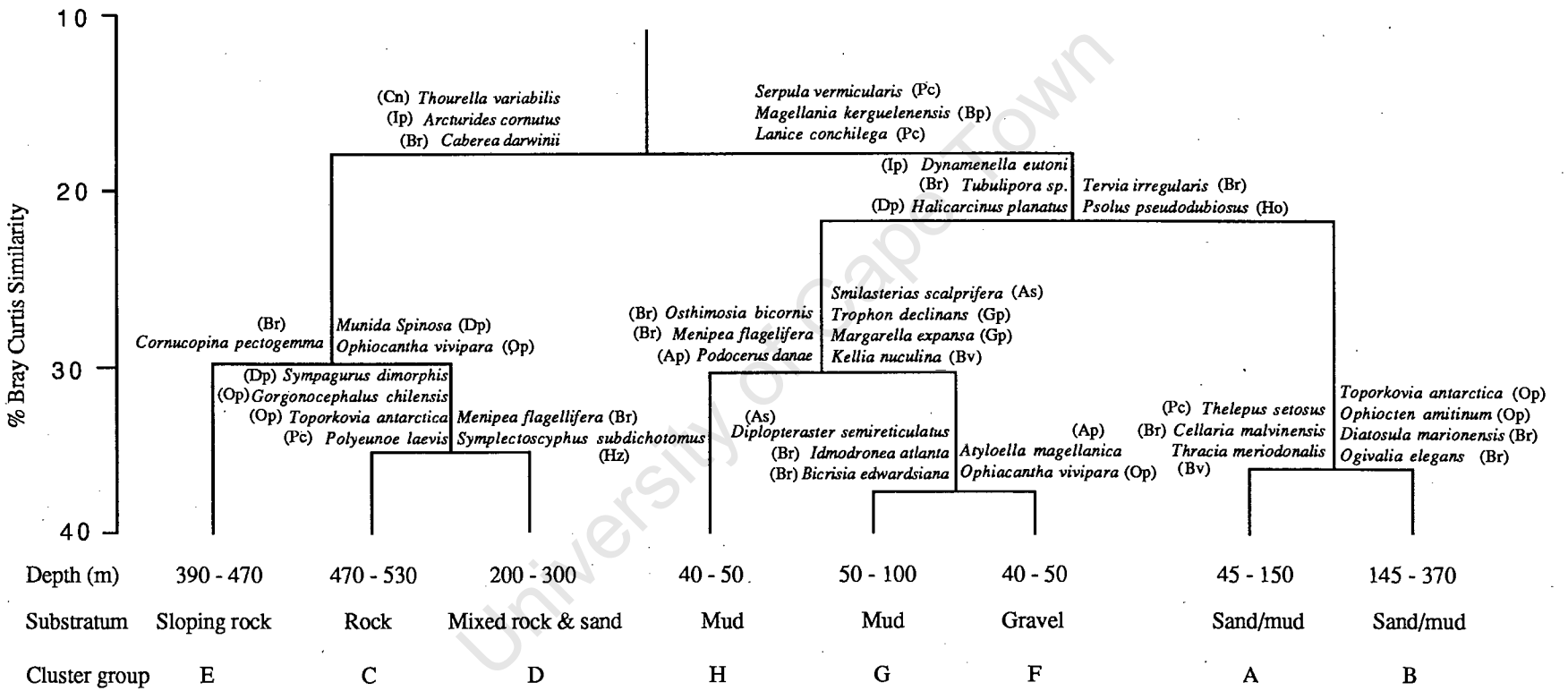

Figure 20: A simplified dendrogram showing only the major groups, their physical characteristics and the diagnostic species of each group or aggregation of groups. Each dichotomy has two sets of diagnostic species, each set being present in the stations of that group but not in the other. The letters in parentheses indicate the higher taxon: Ap = amphipod, As = asteroid, Br = bryozoan, Bv = bivalve, Cn = cnidarian, Dp = decapod, Gp = gastropod, Ho = holothuriod, Hz = hydroid, Ip = isopod, Op = ophiuroid.

this group. Two stations south-east of Marion Island were 60 % similar (group D). They occurred in shallower water (200 - 300 m) and had a substratum of mixed sand and rock, but shared the same major species as those of the previous group. Another group of stations (43% similarity) occurred south-east of Marion Island in depths ranging from 390 - 700 m, on sloping rocky substrata (group E). Sponges, *Ogivalia elegans* (Bryozoa), *Thourella variabilis* (Octocorallia), *Diatosula marionensis* (Bryozoa) and *Cornucopina pectogemma* (Bryozoa) accounted for > 50% of the animals recorded in this group.

Shallow, in-shore: Those communities sampled close inshore to Marion Island in < 100 m depth grouped together to form at least three separate communities. Three of these inshore stations were 43% similar (group F). Each had a gravel bottom and was on the exposed (western) side of the islands. In this group the important species were *Pseudechinus marionis* (Echinoidea), *Nauticaris marionis* (Decapoda), *Margarella expansa* (Gastropoda) and *Ophiacantha vivipara* (Ophiuroidea). Three shallow (50 - 100 m) soft-bottom stations were 42% similar (group G). The important species here were *Allotanais hirsutus* (Tanaidacea), *Halicarcinus planatus* (Decapoda), *Hippothoa* sp. (Bryozoa) and *Thelepus setosus* (Polychaeta). Two very shallow (30-40 m) stations with soft-sediment formed group H, different from the other two inshore groups (45% similarity). These two stations shared *Nauticaris marionis* (Decapoda), *Allotanais hirsutus* (Tanaidacea), *Hippothoa* sp. (Bryozoa) and *Osthimosia bicornis* (Bryozoa) as the dominant species. It was also striking that many of the shallow stations were unique, failing to cluster with other stations at 40% similarity.

Discussion

Samples from the epi-benthic sled provided qualitative information in the form of presence or absence of taxa, and the relative abundance of each. The reliability of this information can be questioned for two reasons. The sled did not operate efficiently on hard, rocky substrata, indeed it was not designed to do so, and might not have given representative samples. Dredging on the shelving, irregular bottom was always a tricky operation. Over the five-year duration of this study, four dredges were snagged on rocks and lost, despite there being a safety release mechanism. While most of the diverse samples (> 60 spp.) were taken from rocky

substrata, so were the least diverse samples; the variability of rocky substratum samples was greater than that of any other substratum type. Of the stations which showed less than 40% similarity to any other station, 80% were of rocky substrata. While this variability might be a feature of rocky substrata, the difficulty in sampling this habitat must be considered as a likely cause of the sample variability. Unfortunately there was no better method of sampling the rocky substrata.

The sled, with a mesh size of 2.0 mm, is a selective sampler. Some meiofauna less than 2 mm were retained in the 1 mm sorting tray, but the fraction lost from the sled could not be determined. Only the macrofauna could be sampled reliably. The accuracy of the community patterns deduced from these samples was severely biased by the exclusion of the meiofauna, particularly for soft-substrata. It was practise to repeat a tow where it was evident that a significant proportion of the sample was lost through the mouth of the sled, particularly as the ship surged while the sled was close by. This event might have occurred out of sight on some occasions, although a bias caused in this way was probably less significant than the previous sources of error.

One of the principal objectives of taking submarine photographs was to visually assess the type of substratum. The classification of substratum was based on information from the photographs and on the analyses of samples brought up by the sled. Repeated photographs at each station also gave a measure of the dispersion of conspicuous taxa. However, several taxa were repeatedly not found on photographs at stations where they were found in sled samples. These groups included small species (gastropods, isopods and amphipods), clumped species (ophiuroids) and burrowing species (polychaetes). The photographs did show a high ocurrence of fish, which were seldom trapped in the sled, and gave a considerably different and incomplete impression of the benthic invertebrates. For this reason, analyses of abundance and presence/absence data were restricted to the sled samples.

The macrobenthic diversity at stations sampled at the Prince Edward Islands is considerably less diverse than that recorded on the Antarctic continental shelf. For that area the number of species per station was typically 60 to 110 (Richardson and Hedgpeth 1977), whereas at the Prince Edward Islands the corresponding values were 15 - 60. Saunders (1968)

and Lowry (1975) concluded that the diversity of Antarctic benthos was due to the stability of the physical environment. While the physical environment is stable at the Prince Edward Islands too, it is the youth of these islands and its isolation which most likely account for the lower macrobenthic diversity than elsewhere in the southern ocean.

The similarities of stations based on the ranked species abundance allowed several communities to be distinguished. Each of these communities corresponded to a particular depth range and/or substratum type. Trends in ecological indices, however, could not be found - species richness, feeding type composition, and the occurrence of major taxa did not differ with respect to depth or substratum type. The problem with recording species richness precisely, particularly on rocky substrata as discussed earlier, might have masked real differences in diversity. Moderately high diversities were encountered in some of the deep rocky stations and, despite this finding not being consistent, it may be a feature of these stations. The percentages of filter feeders and deposit feeders, because they are calculated from a large number of species, are less likely to be biased. These show that, even for muddy substrata, filter-feeding is the dominant form of nutrition among the benthic species. In this respect, the macrobenthos of the Prince Edward Islands is similar to that of the Antarctic where sessile filter feeders dominate, namely sponges, bryozoans and cnidarians on rocky substrata, and bivalves, brachiopods and filter-feeding polychaetes on or in soft-sediments. The errant forms at the Prince Edward Islands were dominated by echinoderms, with crustacea, particularly isopods and amphipods, being more important in shallower water. *Nauticaris marionis* deserves a mention as it was abundant throughout the region.

Examining the distribution of taxa among the substatum types yields confusing patterns. While, for instance, bryozoans were more conspicuous on rocky substrata, this phylum was well represented in all samples. Similarly, polychaetes occurred on both soft and hard substrata. A more useful approach is to examine the species which contribute most to the dissimilarity between communities which have different physical characteristics. This yields the following description of the broad communities of the Prince Edward Islands (figure 20).

(1) Deep, rocky communities formed a group separate from other groups, being distinguished by the presence of the cnidarian *Thourella variabilis*, an isopod *Arcturides*

cornutus which is associated with *T variabilis*, and the bryozoan *Caberea darwinii*; and an absence of the polychaetes *Serpula vermicularis* and *Lanice conchilega* and the brachiopod *Magellania kerguelenensis*.

(2) The remaining stations were all shallow and split into two groups. A very shallow, in-shore component (40 - 100 m) was characterised by the presence of the isopod *Dynamenella eatoni*, the crab *Halicarcinus planatus* and the bryozoan *Tubulipora* sp., whereas the deeper groups had the bryozoan *Tervia irregularis*, and the holothurian *Psolus pseudodubiosus*.

All these groups subdivided further according to their average Bray-Curtis similarity, and in each case the subdivisions could be distinguished by the depth, substratum type or degree of exposure. The diagnostic scheme presented in figure 20 at each of the dichotomies is not entirely objective. Simply listing the species which contribute most to the dissimilarity favours highly abundant species, which might be present in both groups albeit in very different proportions. For this reason the diagnostic species include less abundant species which occurred in one group but not at all in the other. Their collective presence is thus diagnostic. Because of the confusing array of species available for this task, only the best-described major taxa were searched for indicator species.

Picken's (1985) list of major factors affecting Antarctic benthic community composition includes organic input, besides depth and substratum type which had already been shown to influence the Prince Edward Island communities. Although spatial variations in organic flux to the sediments of the Prince Edward Islands have not been established, the overlying water does support high primary production, and its the effect on the benthos must be considered. Dayton and Oliver (1977) demonstrated differences between communities bathed by oligotrohic and eutrophic water at McMurdo Sound, Antarctica. Eutrophic water supported a diverse and abundant benthic fauna, while the opposite was true for oligotrophic water.

Two major sources of energy for the Prince Edward Island benthic communities can be identified, viz. (1) downward flux of phytoplankton and (2) material imported by the Antarctic Circumpolar Current (ACC). Whereas the sub-Antarctic surface water is generally poor in chlorophyll, the pelagic water around the islands is often rich in chlorophyll of diatom origin. This is true of all sub-Antarctic Indian ocean islands. At the Prince Edward islands the

dominant species is *Chaetoceros radicans* which has reached phenomenal densities of 10^9 cells.m^{-3} (Boden 1988). I suggested that the reason for the recurrence of this species is due to its habit of forming resting spores. At the advent of unfavourable conditions the resting spores develop and sink to the shallow sediments, from where a dormant population can re-seed surface water. The benthic community may thus be in a position to receive a significant proportion of surface production. The concentration of *Chaetoceros* diatom cells at the sediment-water interface has been found to exceed that of the overlying euphotic water in the southern Benguela (Pitcher 1986). If this sinking process is of a similar magnitude at the Prince Edward Islands, it would imply that enormous quantities of diatom cells feed the benthos, an argument supported by the high proportion of filter-feeders. Although the diversity of this benthic community is impoverished, due perhaps to its geographic isolation and relative youth, a quantitative survey is likely to reveal a high standing crop. The percentage of ground covered by organisms was high, 32.5% on average, reaching a peak in shallow water. Few studies could be found with which to compare this value. Thorson (1957), however, estimated that, on average, macrofauna occupy 10% by area of the sea bottom, reaching a maximum in the littoral zone. At 9 stations the ophiuroid numbers counted from 5 - 12 photographs exceeded 30 individuals.m^{-2}, with an average of 193 at station 4. Similarly densities in excess of 20 individuals.m^{-2} were not unusual for *Nauticarius marionis*.

The role of the shrimp *Nauticaris marionis* in coupling benthic and pelagic food webs was investigated by Perissinotto and McQuaid (1990). This shrimp, which was found at the majority of stations, forms a major fraction of the diets of the Gentoo penguin (26% by mass), the Macaroni penguin (5% by number), the rockhopper penguin (9% by number), the Imperial cormorant (19% by mass) and the fish, *Paranotothenia magellanica* (4% by mass) (Perissinotto and McQuaid 1990). *Nauticaris marionis* in turn feeds principally on foraminiferans, bryozoans, octocorals, harpacticoid and calanoid copepods and euphausiids. These two latter pelagic sources of food suggest that this benthic, or suprabenthic, shrimp may be in a position to predate on downwardly migrating zooplankton, particularly euphausiids and copepods. The vertical migrators which would normally occur at > 300 m depth during daylight hours reach the shallow island plateau at a depth of < 200 m, should they pass over it at the break of day. The

success of *Nauticaris marionis* might to some degree depend upon material introduced from the adjacent pelagic system, in addition to the stocks of benthic prey.

The study of the biogeographic affinities of the Prince Edward Island benthic fauna remains an uncomplete and major undertaking. White (1984) lists the species characteristic of sub-Antarctic islands as one of four principal biogeographic components of Antarctic benthic fauna. The agent of dispersal is the ACC, which would have carried the Islands' present fauna from southern South America and from the Scotia Arc. The Prince Edward Islands do interupt the west-wind drift and oceanographers have speculated on what effect this might be (Allanson et al. 1985, Boden 1988, Duncombe-Rae 1989, Perissinotto and Duncombe Rae 1990). It is likely that a Von Karman Street (a wake embedded with eddies) develops on the lee side of the islands. Whether or not a stationary eddy, in the sense of a Taylor column, is trapped at the islands is a theory which has yet to be tested. Should such an eddy exist, it would have important consequences for the dispersal and recruitment for those benthic species with pelagic larval stages. Both the existence of an eddy and the occurrence of benthic species with pelagic larvae are questions which would be pertinent to an investigation into the adaptations of the fauna of the Prince Edward Islands to their insular existence.

References

Allanson B.R., B. Boden, L. Parker and C. Duncombe Rae (1985) A contribution to the oceanology of the Prince Edward Islands. In: *Antarctic nutrient cycles and food webs*, W.R. Siegfried, P.R. Condy and R.M. Laws, editors, Springer-Verlag, Berlin, pp. 38-45.

Boden, B.P. (1988) Observations of the island mass effect in the Prince Edward Archipelago. *Polar Biol.* 9, 61 - 68.

Dayton, P.K. and J.S. Oliver (1977) Antarctic soft-bottom benthos in oligotrophic and eutrophic environments. *Science* 197, 55 - 58.

De Villiers, A.F. (1976) Littoral ecology of Marion and Prince Edward Islands (Southern Ocean). *S. Afr. J. Antarct. Res.* Supplement 1, 1 - 39.

Duncombe Rae, C.M. (1989) Physical and chemical marine environment of the Prince Edward Islands (southern ocean) during April/May 1987. *S. Afr. J. Mar. Sci.*, 8, 301-311.Lowry, J.K. (1975) Soft bottom macrobenthic community at Arthur Harbour, Antarctica. *Antarct. Res. Ser.*, 23, 1 - 19.

Lutjeharms, J.R.E. and H.R. Valentine (1984) Southern Ocean thermal fronts south of Africa. *Deep Sea Res.* 31(12), 1461 - 1475.

McDougall, I (1971) Geochronology. In: *Marion and Prince Edward Islands. Report on the South African Biologicl and Geological Expedition / 1965- 1966*, Van Zinderen Bakker, E.M., J.M. Winterbottom and R.A. Dyer, editors,. A.A. Balkema, Cape Town, 427 pp.

Perissinotto, R. (in press) Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edwrd Archipelago (southern ocean). *Mar. Ecol. Prog. Ser.*

Perissinotto, R. and C.M. Duncombe Rae (1990) Occurrence of anticyclonic eddies on the Prince Edward Plateau (South Ocean): effects on phytoplankton biomass and production. *Deep-Sea Res.*, 37(5), 777-793.

Perissinotto, R and C. McQuaid (1990) Role of the sub-Antarctic shrimp *Nauticaris marionis* in coupling benthic and pelagic food-webs. *Mar. Ecol. Prog. Ser.*, 64, 81 - 87.

Picken, G.B. (1985) Benthic research in Antactica: past, present and future. In: *Marine Biology of polar regions and effects of stress on marine organisms*, J.S. Gray and M.E. Christiansen, editors, John Wiley and Sons Ltd, Lonon.

Pitcher, G.C. (1986) Sedimentary flux and the formation of resting spores of selected *Chaetoceros* species at two sites in the southern Benguela system. *S. Afr. J. mar. Sci.* 4, 231 - 244.

Richardson, M.D. and J.W. Hedgpeth (1977) Antarctic soft-bottom, macrobenthic community adaptations to a cold, stable, highly productive, glacially affected environment. In: *Adaptations within Antarctic ecosystems*, G.A. Llano, editor, Gulf Publishing Co., Houston, 181-196.

Saunders, H.L. (1968) Marine benthic diversity; a comparative study. *Am. Nat.* 102, 243 - 282.

Thorson, G. (1950) Reproduction and larval ecology of marine bottom invertebrates. *Biological Reviews* 25, 1 - 45.

Van Zinderen Bakker, E.M., J.M. Winterbottom and R.A. Dyer (editors) (1971) *Marion and Prince Edward Islands. Report on the South African Biologicl and Geological Expedition / 1965- 1966.* A.A. Balkema, Cape Town, 427 pp.

White, M.G. (1984) Marine benthos. In, *Antarctic Ecology vol 2*, M. Holdgate, editor, Academic Press, London.

Zar, J.H. (1984) *Biostatistical analysis.* Prentice-Hall, Inc., Englewood Cliffs, N.J.

Conclusions

To draw a single conclusion from the diverse chapters in this thesis is quite impossible. Instead, I intend to discuss the relevence of the findings in terms of the several points of interest which I outlined in the introduction. It is fair to say that during the past three years, or more, our understanding of the functioning of the marine communities of the Prince Edward Islands has altered considerably. My own work formed only a very small part of the effort and ideas which have brought about this change. Very few of the original questions are resolved, rather they have merely shifted focus and new hypotheses present themselves for testing. These I will discuss in turn.

The theory presented in chapter 1 on the cause of diatom blooms at the Prince Edward archipelago is different from that suggested previously. I contend that, *in so far as diatom growth is concerned, the physical structure of the water mass at the archepelago is not different from that of the adjacent oceanic water. The cause of the repeatedly observed blooms is not due to a physical feature in the water unique to the archipelago. While the potential for diatom bloom development is uniform everywhere in this region of the ocean, it is the presence of a population of diatom resting spores which seeds blooms locally and repeatedly.* Dr L. Hutchings (pers. comm., Sea Fisheries Research Institute, Cape Town) and Dr R. Perissinotto (pers. comm., Southern Oceans Group, Rhodes University, Grahamstown) are of the opinion that the development of a bloom will, nonetheless, require a mechanism to retain the plankton in the vicinity of the archipelago in order to account for the observed distribution of the blooms and to allow the spores to fall on the shallow sediment. However, it must first be demonstrated that a current exists over, or adjacent to, the archipelago which will rapidly remove plankton from the ~1500 km^2 area should a retention mechanism not exist. I suggest that to resolve this issue, firstly, no amount of speculation on the currents will be useful, unless these currents are measured by drogues, moored current meters or a ship-based acoustic doppler current profiler. Although we know the general velocity parameters of the Antarcic Circumpolar Current, its meso-scale characteristics around the islands are not resolved. Secondly, the concentration of resting spores should be measured in the sediment and at the sediment-water interface with a

box-core, and the downward flux of resting spores should be measured during a bloom with moored sediment traps.

I have searched in vain through all the available evidence to reach a conclusion on what the physical reason for the development of the bloom might be, nonetheless I still suspect that these diatoms are light-limited, and that their growth depends on the stability of the water-column. This issue is indeed still very topical with respect to Antarctic phytoplankton.

The abrupt intrusion of the islands in the deep Indian Ocean affects the marine communities in two ways. Firstly, it provides a purchase for species which would otherwise not exist there. This is true not only for birds and shallow marine invertebrates, but also for kelp and diatoms which are major producers. The role of kelp in the food-web, as discussed in chapter 3, is limited to fueling a littoral microbial community. At first glance the role of diatoms appeared equally disappointing, for the desert-like sub-Antarctic ocean (mean chlorophyll ~ 0.3 mg Chl-*a*.m^{-3}) supports too few herbivores to take advantage of the islands' diatom blooms (up to 2.2 mg Chl-*a*.m^{-3}) (Perissinotto, in press). Many of the copepods and euphausiids at the Prince Edward Islands, which were examined in chapter 2, were a mixed bag more commonly found in either Antarctic or sub-tropical water. The euphausiids were found to be in poor condition, judging from their low fat content at the end of summer when they would be expected to be replete with lipids. It appears as if those species occuring at the islands originate from populations centred on either the Sub-Tropical Convergence or the Antarctic Polar Front, which are highly productive regions. Measurements of zooplankton abundance along a north-south transect across both fronts might confirm that herbivores are more successful at the fronts either side of the Prince Edward Islands.

However, it now appears as if sinking diatoms might fuel a large benthic biomass (Perissinotto and Boden 1989), as does eutrophic water at the Antarctic ice-edge. Similar to that of the Antarctic, the benthic community of the Prince Edward Islands is dominated by filter-feeders. The abundant penguins and cormorants are utilizing the benthic resources, thus indirectly benefitting from the blooms. These speculations require confirmation by a detailed quantitative investigation of the organic flux to the sediment and of benthic standing stocks.

Secondly, the interruption of the ACC by the islands is the basis for the 'conveyer-belt' effect described by Perissinotto (1989). He pointed to the possibility that the fauna of the archipelago removes material from the water-column as it passes by, and that this source of energy might be more important than the *in situ* production.

References

Perissinotto, R. (in press) Mesozooplankton size-selectivity and grazing impact on the phytoplankton community of the Prince Edwrd Archipelago (southern ocean). *Mar. Ecol. Prog. Ser.*

Perissinotto, R (1989) The structure and diurnal variations of the zooplankton of the Prince Edward Islands: implications for the biomass build-up of higher trophic levels. *Polar Biol.*

Perissinotto, R and B.P. Boden (1989) Zooplankton-phytoplankton relationships at the Prince Edward Islands during April/May 1985 and 1986. *S. Afr. J. Antarct. Res.*, 19(1), 26 - 30.